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Physiological effects of boron on wheat

HELEN S. MORRIS

(WITH PLATES 1–2 AND FOUR TEXT FIGURES)

In recent years considerable work has been done in an attempt to discover the rôle which the element boron plays in plant metabolism, and the results of this work may be divided into three main groups. These consist of observations on the necessity of the element in minute quantities for the normal and healthful development of plants, its toxicity in higher concentrations, and finally a so-called stimulating effect which it exhibits when present in optimum concentration.

The necessity of boron for the healthful development of plants has been demonstrated by a number of authors working on various species. Mazé (1919) stated that boron, fluorine, and iodine were necessary for the complete development of corn, and that the absence of boron resulted in more immediate and more serious injury than did the lack of either of the others. Warington (1923) demonstrated the necessity of boron for the broad bean and clover and remarked on the similarity existing between the rôle of boron in plant life and that of vitamines in animal life. This similarity was not based on chemical nature, but on the fact that both substances were necessary for healthy development, both were needed in minute quantities, and both had to be supplied continuously throughout the life of the organism. Brenchley and Thornton (1925) showed that boron was necessary for the formation of nodules on the roots of *Vicia faba*. The suppression of the characteristic root tubercles in boron-deficient solutions was found to be due not to lack of infection, since the activities of the nitrogen-fixing bacteria were not greatly curtailed in the absence of this element, but to the fact that the vascular strands of the host degenerated. As a result, the bacteria were deprived of their accustomed nutritive material, and were forced to parasitize the meristematic cells in the nodule, thus effectually preventing its further development.

Brenchley and Warington (1926) found that *Vicia faba*, when deprived of boron, not only failed to develop root nodules, but also exhibited apical injury, and died prematurely. Concentrations of boric acid containing 0.07 ppm. of boron or more were sufficient to produce healthy apical growth, but the supply had to be constantly renewed. Warington (1926) studied the effects of boron deficiency on the anatomical structure of *Vicia faba* and found that if boron were not supplied in quantities greater than 0.08

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ppm., the root system became thick and stunted, the flower buds withered and dropped off, and the injury traveled down the plant from the apex toward the root. There was a breaking down of cambium and all meristematic tissue, as well as of phloem, xylem, and ground parenchyma. Sommer and Lipman (1926), in a comprehensive study of mustard, flax, Castor bean, sunflower, and barley, supplied photographic evidence of the general necessity of boron for higher green plants. By removing the seed remnants from the young seedlings they demonstrated that boron was needed early in the development of the plant, but that 0.5 ppm. of boron was adequate for the first few weeks and in some cases for the life of the plant. Swanbeck (1927) and McMurtrey (1929) found that boron was essential for the development of tobacco. Plants deprived of it exhibited typical apical withering and a tendency to form new branches in the axils of the leaves. These abnormal branches withered almost as soon as they were formed. Johnston and Dore (1929) demonstrated the necessity of boron for tomatoes grown in culture solutions. The plants grown in boron-deficient solutions showed a characteristic apical injury as well as unhealthy root development and degeneration of conducting tissues. Haas (1930) reported that boron was essential for the growth of citrus trees, and that trees deprived of it developed abnormal symptoms within two years but were capable of recovery when traces of boron were added. Johnston and Fisher (1930), by placing tomato plants in boron-deficient solutions at the time of blossoming, demonstrated that the element was essential for fruit setting. Only one-fourth as many fruits set in the boron-deficient solutions as in the controls, and these fruits were covered with darkened areas of dead cells.

The toxicity of boron in higher concentrations has been frequently demonstrated, both by laboratory culture methods and by field experiments. Agulhon (1910) found that wheat seeds could be considerably retarded in germination if they were soaked for six hours in a solution containing five grams of boric acid in a liter of water (850 ppm. of boron). His work with various agricultural plants brought out the fact that the toleration range varied with individual species and with experimental conditions. Thus wheat grown in water cultures was not poisoned by solutions containing less than 20 ppm. of boron, whereas wheat, oats, and radishes grown in sand cultures showed toxic effects with concentrations as low as 5 ppm. The greater toxicity of boron in sand cultures he believed to be due to surface concentration effects resulting from evaporation. There was greater toleration of boron in soil than in sand, a fact which he attributed to the possible fixation of boron by the calcium in the soil in the form of insoluble borates. In the soil cultures, differences in toleration were exhibited by different plants, corn being poisoned by concentrations above

10 ppm., radishes by concentrations above 25 ppm., and peas and vetch apparently capable of withstanding concentrations up to 50 ppm.

A similar variation in toxic effects was observed by Brenchley (1927), who found that barley was definitely poisoned by 4 ppm. of boron and was sensitive to concentrations as low as 0.4 ppm., whereas peas could endure concentrations of from 20 to 40 ppm. Her results indicate a general toxicity of boron down to a concentration of 20 ppm., and in many cases lower concentrations. Swanbeck (1927) reported that a concentration of 68 ppm. of boron as boric acid was toxic to tobacco grown in nutrient solutions. The work of Collings (1927) on the soy bean presented additional evidence for the toxic effect of boron on germination of seeds and also for the greater toxicity of the element in sand than in soil cultures. He reported a similarity in the toxicity of potassium borate, sodium borate, and boric acid that indicated that the concentration of boron in the culture solution was the controlling factor in toxicity. Johnston and Dore (1929) in their work on tomatoes reported toxic symptoms with solutions containing 5.5 ppm. of boron. Haas (1929) found that 6 ppm. of boron was toxic to lemon and orange seedlings grown in Hoagland's solution, and that concentrations above 50 ppm. in irrigation water were highly toxic to lemon trees grown in soil. An ash analysis of the affected plants showed a decrease in calcium content and an increase in potassium content compared with the control plants. He reported that ferric sulphate had an ameliorating influence on this boron poisoning and suggested that the effect might be of a catalytic nature or due to precipitation.

A great number of field experiments have also been reported on boron toxicity. These experiments have largely been stimulated by the destruction of citrus orchards by boron impurities in irrigation water (Kelley and Brown, 1928), and by the failure of the potato crop in 1919 as a result of a borax impurity in the newly exploited potash fertilizers obtained from the Searles Lake deposits (Blair and Brown, 1921). Blair and Brown (1921) found that the potato yield is decreased to one-half by an application of 100 pounds of borax to an acre, to one-fourth by 200 pounds, and to one-twentieth by 400 pounds. They also reported that an application of 5 pounds per acre seriously retarded the growth of corn. Skinner and Allison (1923) found that cotton was seriously injured by an application of 20 pounds to an acre. Skinner, Brown, and Reid (1923) reported that corn and beans were more susceptible to borax injury than were potatoes, and that an application of 10 pounds to an acre was sufficient to decrease the germination of bean seeds by 50 per cent.

The symptoms of boron toxicity in general differ from those due to its absence, in that the signs of injury appear first at the base of the plant and

travel progressively upward, whereas in boron deficiency the first signs of injury occur at the meristematic apices. Toxicity is evidenced by the destruction of chlorophyll, and also crinkling, burning, and marginal curling of leaves. Haas (1929) reported symptoms of toxicity in lemon to consist of chlorosis, marginal burning, mottling, and the formation of resinous spots on the ventral surfaces of the leaves, followed by their early abcission. He stated, however, that there were no changes in the vascular anatomy as reported by Warington (1926) for broad beans grown in boron-deficient solutions. Collings (1927) reported similar symptoms for the soy bean, remarking that, although the injury advances progressively up the plant, it never appears in the young, actively dividing tissue.

The data are less uniform in regard to stimulation effects which boron produces when present in optimum concentrations. Agulhon (1910) found that there was a marked increase in the growth of higher plants in definite optimum concentrations of boric acid. He described the effect as represented by a curve, at first ascending under the influence of minute concentrations, up to an optimum concentration, then descending under the influence of toxic concentrations to a lethal concentration at which any growth is impossible. He found that the optima differed with different plants, that for wheat lying between 2.5 and 10 ppm. of boron. No definite optimum could be found for vetch, all the concentrations which were non-toxic producing equal growth. Because of the low concentrations at which optimum growth occurred, Agulhon classed boron as a catalytic element.

The curve described by Agulhon has been substantiated by the work of later investigators. For a number of plants, definite concentrations of boron have been found to produce a marked increase in growth, irrespective of whether or not the element has been proved to be essential. These concentrations may be considerably higher than those which are sufficient to prevent visible symptoms of boron deficiency. Such concentrations have frequently been called stimulating; but whether this phenomenon is truly stimulation, by which we imply supra-normal metabolism, or rather simply a high growth rate due to an optimum concentration of a nutrient substance, is questionable. Brenchley (1927) reported that peas exhibited optimum growth in 2 ppm. of boron, and yellow lupines in 3.5 ppm. Brenchley and Warington (1926) found that 0.4 ppm. of boron was stimulating to *Vicia faba*. Collings (1927) found that the dry weight of soy beans grown to maturity in nutrient solutions was increased by the addition of about 2.5 ppm. of boron and that this stimulation was greater when the boron was applied as boric acid than when it was applied as the borate. This increase in the dry weight was always accompanied, however, by symptoms of toxicity in the leaves, and no such stimulation was observed when the

plants were grown in soil or sand, nor when plants in the seedling stage were used as experimental material. Swanbeck (1927) found 2 ppm. of boron favorable for tobacco, and McMurtrey (1929) reported 0.5 ppm. as optimum for the same plant.

Several cases have been reported of plants which can apparently complete their development in the absence of boron, and which exhibit no stimulation effects when it is present. Agulhon (1910) was unable to find any favorable result when boron was added in the form of small traces of boric acid to cultures of yeast, *Aspergillus*, and Bulgarian ferment. This work, as well as that of Brenchley and Thornton (1925) on *Bacillus radicicola*, seems to indicate a lack of sensitivity on the part of lower plants toward the presence of boron in small quantities. Agulhon (1910) found that vetch was insensitive to any fluctuations in boron concentration below the toxic range, Warington (1923) reported that barley was able to attain optimum growth without the addition of any boron to the nutrient solution, and Brenchley (1927) stated that below the toxic range barley grew equally well in all concentrations down to 0.02 ppm. These results may indicate that some of the higher plants cannot be stimulated by boron, or they may mean that the optimum concentration for these plants is extremely low, and may be produced by the minute traces of the element carried as impurities in the nutrient salts employed.

The experiments described in this paper were undertaken with the purpose of studying various aspects of the physiological effects of boron on the wheat plant. The work was done in the laboratory of plant physiology of Columbia University under the supervision of Dr. S. F. Trelease, to whom the author is indebted for his interest and assistance.

METHODS

The experiments were of two types—the one, testing the effect of boron compounds in single salt solutions on the root growth of very young seedlings, and the other, upon the development of wheat plants grown in nutrient solutions during a period of nine weeks. In the seedling experiments the plants were exposed to the culture solutions for four days. Seeds of pure strain Marquis wheat were soaked in distilled water for three hours, drained, and rinsed thoroughly to remove dust and mould spores. They were then planted with forceps on moist filter paper in large glass culture dishes. Each seed was placed with the grooved side downward, and during this process obviously diseased or abnormal seeds were discarded. After about twenty-four hours, or an interval sufficient to allow the production of a root growth of six millimeters, uniform seedlings were selected and transferred to the culture solutions.

The solutions were prepared by dissolving a weighed amount of the required salt and diluting to a given concentration. The values for these solutions are stated throughout the paper as gram molecules per liter, gram atoms per liter, or as parts per million of solution. At first the water for these experiments was distilled in a Barnstead still, but later it was found necessary to redistill through quartz condensers in order to obtain uniformity of results.

The culture vessels (Trelease and Trelease, 1926) consisted of Pyrex glass beakers of two sizes, the smaller of 300 cc. and the larger of 600 cc. capacity. Paraffined bobbinet was fastened over the tops of the smaller beakers with paraffined linen thread. The smaller beakers were then inserted in the larger ones, and the solutions were poured into these pairs of beakers until both the inner and the outer were filled up to the level of the bobbinet.

The seedlings were then transferred from the germinating dishes with forceps and placed so that their roots extended down through the bobbinet into the culture solution. Twenty-five seedlings were grown in each beaker, and duplicate cultures were used for each concentration so that data for the growth of fifty seedlings were provided in each experiment. With each series one set of controls was grown in distilled water, and two sets in a standard, three-salt nutrient solution containing 0.02 m calcium nitrate, 0.02 m magnesium sulphate, and 0.02 m potassium acid phosphate.

The beakers were covered with watch glasses and transferred to a rotating table in a dark, thermostatic chamber (Trelease, 1925), where they were kept at a temperature of 19° C. for four days. At the end of this time the seedlings were removed, measurements of the central primary root were made, and the mean growth increment for the set was calculated.

Throughout the experiment care was taken not to introduce any impurities into the solutions. All beakers, germinating dishes and graduates were washed in hot, soapy water, rinsed several times in tap water, and finally dipped in hot, distilled water before use.

In the long-time experiment, the plants were grown for nine weeks in a standard nutrient solution to which varying concentrations of borax or boric acid were added. The standard solution contained 0.01 m potassium acid phosphate, 0.005 m magnesium sulphate, 0.005 m calcium nitrate, and 0.00001 m ferrous sulphate. The seeds used were Marquis variety (1930, Saskatchewan) and they were germinated as in the previous experiments. At the end of twenty-four hours the seedlings were transferred to enamelware pans. These pans were arranged on the same principle as the beakers in the seedling experiments. A smaller one, covered with bobbinet, was placed inside of a larger, and the two were filled with distilled water up to

the level of the bobbinet cover. The seedlings were grown for four days in these pans and were then transferred to the culture vessels. This use of enamel-ware pans is not recommended unless the surface of the enamel is entirely free from cracks or other imperfections. It was found in several cases where chipping of the enamel had occurred that the underlying metallic substances were dissolved by the distilled water and were highly toxic to the roots of the seedlings. In subsequent experiments Pyrex oven-ware pans have been employed.

The culture vessels consisted of glazed crocks of 7500 cc. capacity. These crocks were obtained from the General Ceramics Company and were composed of "chemical stone-ware." Each crock was covered with a cement lid perforated with five holes into which were fitted corks similarly perforated with five small holes. The lids and the corks were both well coated with paraffin. The crocks were filled with the solutions and the seedlings slipped through the perforations and secured with cotton so that the shoot extended above the surface of the lid while the roots were suspended in the solution underneath.

Thirteen different solutions were used—one to which no boron was added, six to which it was added in the form of boric acid, and six to which it was added in the form of borax. Two complete series were grown with duplicate solutions; but in one series the culture solutions were renewed every week, and in the other they were unrenewed. To the unrenewed solutions distilled water was added each week to replace the volume lost through evaporation and transpiration. Since the effect of the absence of boron was one of the points under consideration in this experiment, care was taken to use salts of high, tested purity, and the distilled water used was freshly prepared in a new, steam heated Barnstead still.

The crocks were mounted on three rotating tables in the greenhouse and exposed to prolonged illumination by means of one 1000 watt Mazda lamp suspended over each table and turned on from about 3:30 to 10:00 p. m. The temperature in the greenhouse was kept fairly uniform, seldom fluctuating above 25° C. or below 18° C. and for the most time remaining well within these limits. Atmometer readings were kept to measure the evaporation conditions prevailing during the experiment and to check the uniformity of these conditions for the three tables. These readings, obtained from Livingston spherical atmometers, indicated a mean evaporation rate of 19 cc. a day. As an additional precaution to insure environmental uniformity, the crocks were shifted from one table to another each week. At the end of nine weeks the plants were harvested and examined for general growth conditions. The tops of the individual plants and the roots of all the plants in each culture, collectively, were stored in separate

manila bags until they became air-dry. They were then dried in an oven at 100° C. for twenty-four hours and weighed.

RESULTS AND DISCUSSION

At first a number of experimental series were tried in which young seedlings were grown for four days in various boron solutions, and the root elongation was used as a criterion of general growth conditions. This method was found by Trelease and Trelease (1925) to be a simple method of estimating quantitatively the effects of certain solution conditions on plant growth. The general results obtained with this method showed a striking similarity to the data secured later by taking the dry weights of plants grown in nutrient solutions over a period of nine weeks.

Effects of boron on the growth of very young seedlings

The toxic effects of boron on wheat roots. A number of tests were made to determine the effect of various boron compounds, the ranges of toxic concentrations, and the stimulating concentrations, if present. At first borax was used as a source of boron (table 1). Later, experiments were tried with

TABLE 1

Growth of wheat roots in solutions containing varying concentrations of borax. Growth values represent the actual growth increment in each of two duplicate cultures and also their average growth expressed as a percentage of the growth in the standard three-salt solution. The values for the average growth in distilled water for the series represented in this table were 67, 69, and 71 per cent of the growth in the standard three-salt solutions.

GRAM MOLECULES OF BORAX PER LITER	GRAM ATOMS OF BORON PER LITER	GROWTH						
		1A mm.	1B mm.	Per cent	1A mm.	1B mm.	Per cent	Ave. Per cent
0.000001	0.000004	66	63	77	—	—	—	77
0.00001	0.00004	82	81	103	71	74	87	95
0.0001	0.0004	104	106	113	99	95	115	114
0.0002	0.0008	93	97	119	—	—	—	119
0.00045	0.0018	85	101	116	—	—	—	116
0.001	0.004	48	48	60	39	60	60	60
0.0025	0.01	20	20	25	—	—	—	25
0.004	0.016	9	10	13	—	—	—	13
0.0063	0.0252	6	2	5	—	—	—	5
0.01	0.04	2	1	3	—	—	—	3
0.1	0.4	0	0	0	—	—	—	0

boric acid (table 2) and potassium borate (table 3) in order to determine to what extent the effects observed in the borax series might be attributed to the presence of boron. The data for these three sets of experiments have been plotted in figure 1, in which growth is expressed in percentage of the root elongation occurring in the standard, three-salt solution, and the con-

centrations are based on a common scale—the number of gram atoms of boron per liter of solution. One gram atom of boron weighs 10.8 grams.

TABLE 2

Growth of wheat roots in solutions containing varying concentrations of boric acid. Growth values represent the actual growth increment in each of two duplicate cultures and also their average growth expressed as percentage of the growth in the three-salt control. The growth values obtained in distilled water for these experiments were 73, 95, 89, and 81 per cent of the growth in the three-salt solutions.

GRAM MOLECULES OF BORIC ACID OR GRAM ATOMS OF BORON PER LITER	GROWTH									
	1A mm.	1B mm.	Per cent	2A mm.	2B mm.	Per cent	3A mm.	3B mm.	Per cent	Ave. Per cent
0.00001	68	71	76[a]	65	75	90	—	—	—	90
0.0001	69	73	77[a]	77	73	97	60	61	90	94
0.0005	61	74	99	72	72	92[b]	—	—	—	96
0.001	72	74	78[a]	64	68	97	74	74	95[b]	96
0.00215	70	60	93	—	—	—	—	—	—	93
0.00463	52	47	71	—	—	—	—	—	—	71
0.005	44	35	59	—	—	—	—	—	—	59
0.01	31	31	34[a]	28	26	39	—	—	—	39
0.0215	11	11	16	—	—	—	—	—	—	16
0.04634	1	1	1	—	—	—	—	—	—	1
0.1	0	0	0	—	—	—	—	—	—	0

[a] Because of abnormally high values for the nutrient control in this series, it is believed that the percentages for these concentrations are too low. They have, therefore, been omitted in calculating the average.

[b] Values obtained by using double the number of experimental plants—i.e., four beakers with twenty-five seedlings in each.

TABLE 3

Growth of wheat roots in solutions containing varying concentrations of potassium borate. Growth values represent the actual growth increment in each of two duplicate cultures and also their average growth expressed as a percentage of the growth in the three-salt control. The average growth in distilled water in this series was 87 per cent of the growth in the three-salt solution.

GRAM MOLECULES OF POTASSIUM BORATE PER LITER	GRAM ATOMS OF BORON PER LITER	GROWTH		
		1A mm.	1B mm.	Per cent
0.00001	0.00004	68	65	87
0.0001	0.0004	87	89	114
0.0002	0.0008	96	98	126
0.00045	0.0018	90	95	121
0.001	0.004	60	64	80
0.0025	0.01	11	10	14
0.01	0.04	0	0	0

From the tables and the curves plotted in figure 1 it is evident that the three compounds have a decidedly toxic effect when present in concentra-

tions of more than 0.005 gram atom of boron per liter. When the curves are thus plotted on the basis of equivalent boron concentrations, the similarity of the toxic ranges of the three substances is striking. All three curves at the concentration of 0.002 gram atom of boron per liter drop sharply and follow distinctly similar courses. A reduction of approximately 40 per cent of growth was obtained in all three cases at a concentration

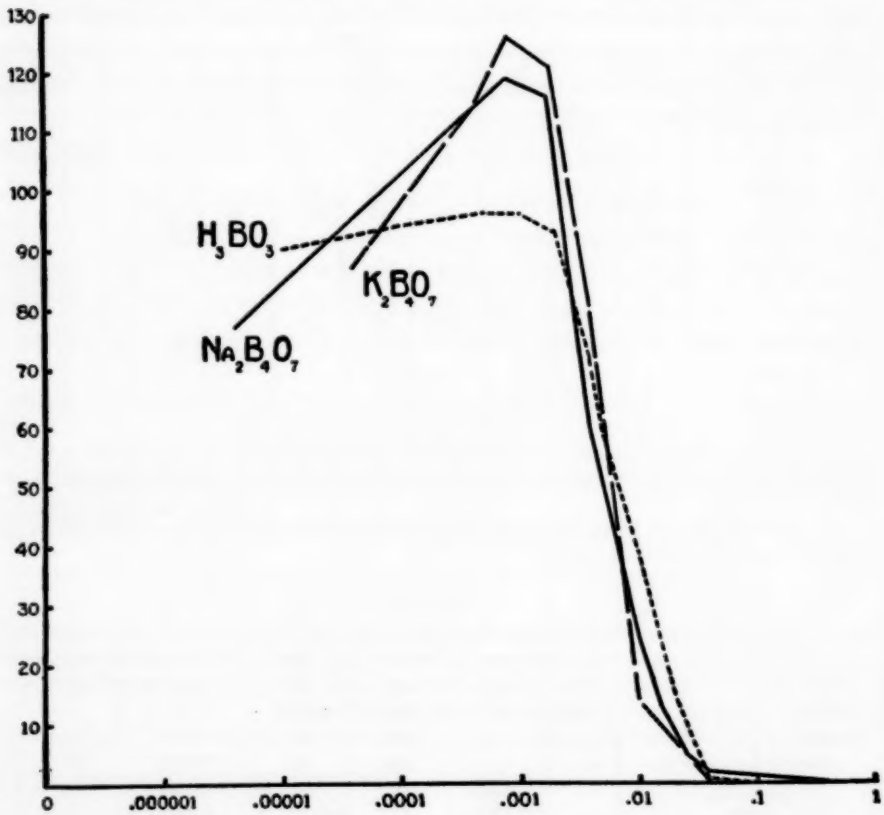

Fig. 1. Elongation of wheat roots in solutions of sodium borate, potassium borate, and boric acid. Ordinates represent percentages of elongation for the standard, three-salt control. Abscissas represent gram atoms of boron per liter.

containing 0.005 gram atom of boron per liter or 54 ppm. of boron; this concentration was supplied by 0.005 m boric acid, 0.00125 m borax, and 0.00125 m potassium borate. A concentration providing 0.04 gram atom of boron per liter (400 ppm.) completely inhibited growth in all three cases.

To further check the similarity in the toxic activity of these compounds, a series was tried using a constant concentration of boron (0.1744

grams or 0.016 gram atom of boron per liter) obtained by mixing borax and boric acid in varying proportions. The results of this experiment (table 4) show that there are relatively small differences in the toxic effects, although the pH values range from 6.4 to 8.8. Borax appears slightly more toxic than boric acid, an observation indicated also by the relative positions of the curves in figure 1. The increase in growth between pH 6.6 and 8.0 appears to be significant. This may indicate a slight conditioning effect of hydrogen-ion concentration upon the degree to which boron toxicity may manifest itself. Or, if the boron toxicity is assumed to be constant, it indicates that this range of hydrogen-ion concentrations is less toxic than are higher and lower hydrogen-ion concentrations.

TABLE 4

Growth of wheat roots in solutions containing 0.1744 grams of boron per liter obtained with mixtures of borax and boric acid in varying proportions. The value for the distilled water cultures was 83 per cent of the growth in the three-salt controls.

GRAM MOLECULES OF BORAX PER LITER	GRAM MOLECULES OF BORIC ACID PER LITER	GROWTH			pH VALUES
		1A mm.	1B mm.	Per cent	
0.00001	0.0160	11	11	15	6.4
0.00005	0.0158	14	15	21	6.6
0.0001	0.0156	15	15	21	7.0
0.0005	0.0140	17	18	25	7.7
0.001	0.0120	16	16	22	8.0
0.0025	0.0060	9	9	13	8.6
0.0035	0.0020	7	7	10	8.8

In studying the toxicity of boron, the question arose as to whether this was an effect such as one might expect in any single-salt solution, or whether it was of a different nature. Osterhout (1908) demonstrated that single-salt solutions were toxic, and that the toxicity of such solutions in most cases might be overcome by the addition of another salt. Later extensive work on antagonism has indicated that the toxicity of many cations may be overcome by the addition of some other cation, and that calcium is particularly effective in such antagonism (McCool, 1913; Osterhout, 1922). Agulhon (1910) reported that the concentrations of boric acid which he used were not so toxic in soil as in sand cultures; and he proposed, as one possible explanation, the fixation of boron in the soil in the form of insoluble borates of calcium. Brenchley and Warington (1926), on the other hand, found that enough boron could be obtained from the relatively insoluble borates of cobalt and calcium to depress the growth of *Vicia faba*.

This question suggested an experiment to test whether calcium is effective in antagonizing boron toxicity. At first an attempt was made to

add varying concentrations of calcium nitrate to a 0.01 m solution of borax; but it was found that, even when the calcium nitrate was diluted to a 0.000001 m concentration, precipitation occurred. Test experiments were then made to find a suitable working concentration of borax that would be toxic, and still not cause precipitation of the calcium. A 0.004 m solution of borax (0.016 gram atom of boron per liter) was finally chosen, and to this concentration were added varying amounts of calcium nitrate. The results of this experiment (table 5) seem to indicate an absence of any signifi-

TABLE 5

Growth of wheat roots in a toxic, 0.004 m concentration of borax to which varying concentrations of calcium nitrate have been added.

GRAM MOLECULES OF CALCIUM NITRATE PER LITER	GROWTH					
	1A mm.	1B mm.	Per cent	2A mm.	2B mm.	Per cent
0.000001	11	10	17	7	7	10
0.00001	11	11	17	10	10	14
0.0001	10	12	17	9	9	12
0.001	8	6	11	7	7	10
0.01	3	3	5	4	3	6
0.1	0	0	0	1	1	1

Growth of wheat roots in a toxic, 0.0196 m concentration of boric acid to which varying concentrations of calcium nitrate have been added.

GRAM MOLECULES OF CALCIUM NITRATE PER LITER	GROWTH		
	1A mm.	1B mm.	Per cent
0.000001	7	9	10
0.00001	7	9	10
0.0001	9	10	12
0.001	9	13	13
0.01	11	13	14
0.1	5	6	7

cant degree of antagonism existing between calcium and boron, and an additive toxic effect with the higher concentrations of calcium. Similar results were obtained (table 5) when calcium nitrate was added, in varying amounts, to a 0.0196 m solution of boric acid (0.0196 gram atom of boron per liter). It is apparent from these data that borax and boric acid are definitely toxic in concentrations that are too low to cause precipitation of calcium, and that there is no antagonism between calcium and either of these substances.

A similar experiment on possible antagonistic effects was suggested by

the report by Haas (1929) that iron, added to a culture solution containing 7.5 ppm. of boron, materially decreased the toxic action of boron on citrus seedlings. Culture solutions were prepared which contained 0.0025 m potassium borate (0.01 gram atom of boron per liter) with the addition of varying concentrations of ferrous sulphate. When concentrations of more than 0.001 m ferrous sulphate were added to the boron solution, a dark green precipitate was formed, and in the 0.001 m solution an orange precipitate was produced. From table 6 it can be seen that the only case in which there is an increase of growth over that of the culture supplied with boron alone is in the 0.001 m solution of ferrous sulphate—the highest concentration used and the only one in which precipitation occurred. In this instance the decrease in toxicity of the solution is apparently due to the removal of a certain proportion of the borate ions by precipitation. Mellor

TABLE 6

Growth of wheat roots in a 0.0025 m solution of potassium borate to which were added varying concentrations of ferrous sulphate. The growth in distilled water was 68 per cent of the growth in the three-salt control.

GRAM MOLECULES OF FERROUS SULPHATE PER LITER	GROWTH		
	1A mm.	1B mm.	Per cent
0.000000	20	17	21
0.000001	20	17	21
0.00001	13	13	15
0.0001	16	19	20[a]
0.001	32	26	34[a]

[a] Concentrations of ferrous sulphate higher than 0.001 m caused the formation of a blue-green precipitate and so were not used. In the 0.001 m concentration an orange precipitate formed and the 0.0001 m solution was tinged with yellow.

(1924) has recorded the formation of ferrous borate in this way by double decomposition with borax and a ferrous salt solution. There is no evidence of any true antagonism existing between iron and boron.

From these experiments it would seem that the toxicity of boric acid and the borates is a special effect characteristic of the boron compounds. It depends directly upon the concentration of boron, irrespective of any balance existing between boron and other substances in the nutrient medium. This casts an interesting light on the conception of boron toxicity.

It is to be expected that boron in single-salt solutions should be toxic, but the curious fact is that it is less toxic under such conditions than are most of the so-called "nutrient" elements. Figures collected from papers published by Trelease and Trelease (1926), Barton and Trelease (1927), and Eisenmenger (1928) indicate that, in single-salt solutions, manganese

chloride, magnesium nitrate, calcium nitrate, and potassium acid phosphate are more toxic than any of the boron compounds used in the experiments described above. A 0.006 m solution of magnesium nitrate permitted 8 per cent as much growth as the control solution, a 0.005 m solution of manganese chloride permitted 2 per cent, and a 0.006 m solution of calcium nitrate permitted 31 per cent, whereas an equivalent concentration of boron in any of its various compounds permits 60 per cent as much growth as the control. Trelease and Trelease (1926) obtained a growth of 77 per cent in a 0.006 m solution of potassium nitrate, while Eisenmenger (1928) found a growth of only 37 per cent of the control in the same concentration of potassium acid phosphate, indicating that the toxicity of these metallic salts in simple solutions is conditioned by the anion constituent of the salt. A comparison of boron with these other nutrient elements may be safely made on the basis of these figures because the methods employed in the boron experiments were the same as those used by these previous workers, and the experimental material was wheat in each case.

All of these authors found that the toxicity of these salts is greatly reduced when other salts are added, and have thus demonstrated antagonism between various pairs of ions. No such relationships are observable in the results obtained with boron. The toxicity remains practically constant, irrespective of the form of the boron compound; no antagonism exists between calcium or iron and boron, and as will be shown later in the long-time experiments, the toxicity in a balanced nutrient solution is practically the same as that in a single-salt solution.

Optimum boron concentrations for root growth of seedlings. From tables 1, 2, and 3, and figure 1, it is apparent that there is an optimum range of boron concentrations below which there is a gradual decrease in growth with decreasing concentration, and above which any increase in concentration causes a decided drop in the growth rate as toxicity becomes an important factor. This range includes concentrations of boron between 0.0002 and 0.002 gram atom of boron per liter or between 2 and 20 ppm., and is the same for all three boron compounds.

The amount of growth produced in this optimum range of boron concentrations, however, is decidedly different with the boric acid and the two alkaline borates. The growth in the optimum boric acid concentrations, although it exceeds that in distilled water, does not surpass the growth in the three-salt, standard solution. In the optimum concentrations of the alkaline borates, on the other hand, the growth values indicate marked stimulation. A study of the hydrogen-ion concentration in these optimum ranges indicates that the best growth in the alkaline borates occurs at about pH 8.5, whereas the optimum growth in the boric acid cultures occurs at pH 6.8.

A question here presented itself as to whether the borate ion is stimulating in itself, under the conditions of these experiments, or whether the increase in growth, found here only in the cultures containing the alkaline borates, might not be due simply to the alkalinity of the medium. In order

TABLE 7

Growth of wheat roots in solutions of sodium carbonate, sodium bicarbonate, and sodium chloride. The distilled water values for the three series were respectively 88, 87, and 90 per cent of the growth in the three-salt control.

GRAM MOLECULES OF SODIUM CARBONATE PER LITER	GROWTH			pH VALUES
	1A mm.	1B mm.	Per cent	
0.000005	61	70	88	7.0
0.00005	76	79	104	7.2
0.00007	81	80	108	7.6
0.00014	86	83	113	8.8
0.00019	90	84	116	8.8
0.0005	94	94	125	8.8
0.005	1	1	1	8.8
GRAM MOLECULES OF SODIUM BICARBONATE PER LITER	GROWTH			pH VALUES
	1A mm.	1B mm.	Per cent	
0.0001	70	68	108	6.6
0.0005	85	89	114	7.1
0.001	83	87	113	7.6
0.002	65	67	103	7.8
0.005	61	59	94	8.2
0.01	30	20	39	8.4
0.1	0	0	0	8.4
GRAM MOLECULES OF SODIUM CHLORIDE PER LITER	GROWTH			pH VALUES
	1A mm.	1B mm.	Per cent	
0.00001	75	78	96	6.6
0.0001	75	80	97	6.6
0.001	73	80	96	6.6
0.005	70	70	88	6.6
0.01	57	57	71	6.6
0.05	2	3	4	6.6
0.1	0	0	0	6.6

to test the effect of other alkaline salts on the growth of wheat, two experiments were made with solutions of sodium carbonate and sodium bicarbonate, and a third with sodium chloride, for purposes of comparison. The results are shown in table 7. In figure 2 the growth values for these

three sets of cultures are plotted with the values for sodium borate, using, as a common basis, the sodium concentration of the four compounds. The graph and table bring out very clearly the differences in the stimulating power of these four sodium salts. With sodium borate there is marked stimulation at pH 8.6; with sodium carbonate, at pH 8.8; with sodium bicarbonate, a slightly lower stimulation between pH 7.1 and 7.8. In the case

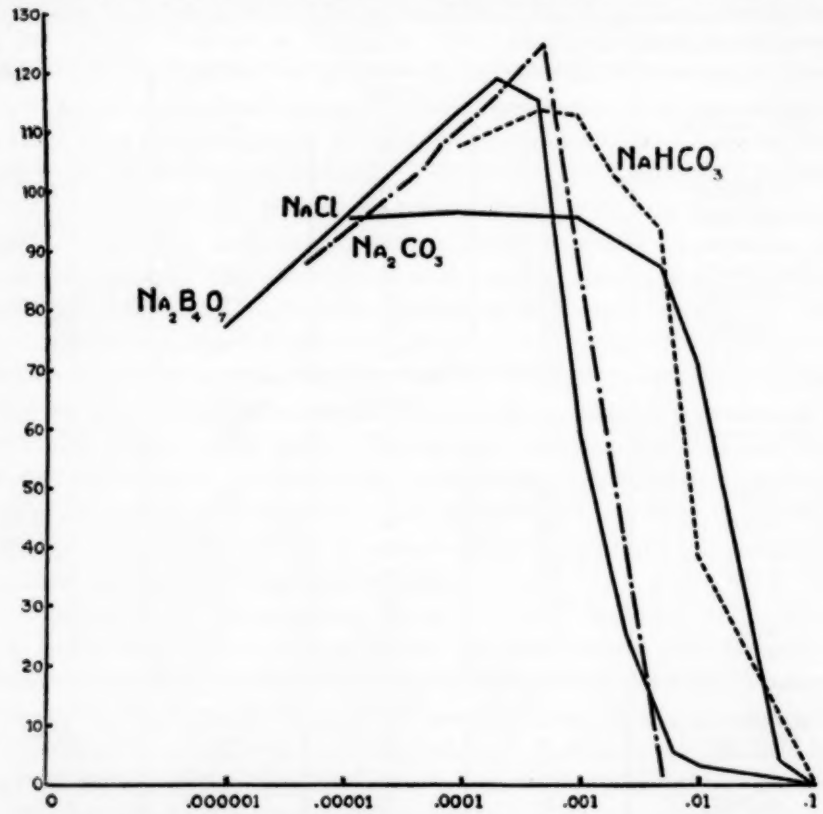

Fig. 2. Elongation of wheat roots in solutions of sodium borate, sodium carbonate, sodium bicarbonate, and sodium chloride. Ordinates represent percentages of elongation for the standard, three-salt control. Abscissas represent gram atoms of sodium per liter.

of the neutral sodium chloride, where the pH value for all the concentrations is 6.6, there is no evidence of stimulation apparent. This difference between the effects of the alkaline and neutral sodium salts on the growth of wheat roots is suggestive of the difference between the results obtained with the alkaline borates and those obtained with boric acid—solutions of the latter having about the same pH value as solutions of sodium chloride.

Effects of boron on wheat plants grown for nine weeks in nutrient solutions

The difficulty in the interpretation of the stimulation in the experiments dealing with the earliest phases of seedling development lies in the fact that the plants are still dependent on inorganic nutrients as well as organic food stored in the seed. Inasmuch as a three-salt solution in itself might be considered stimulating under these circumstances, it is difficult to know whether the distilled water cultures or the three-salt solutions should be considered as the controls on which to base stimulation results. For this reason plans were made for growing wheat plants in boron cultures over a longer period of time in order to determine possible stimulating effects of the boron compounds with a greater degree of precision.

In this experiment wheat plants were grown in a standard nutrient solution, to which boron, in the form either of borax or boric acid, was added.

TABLE 8

Dry weights of the tops of wheat plants grown for nine weeks in renewed and unrenewed solutions containing varying quantities of boron, supplied either as boric acid or borax.[a]

NO.	GRAM ATOMS OF BORON PER LITER	PPM. OF BORON	pH_1	RENEWED SOLUTIONS OF BORIC ACID		UNRENEWED SOLUTIONS OF BORIC ACID	
				Weight mgm.	pH_2	Weight mgm.	pH_2
1	None	0.0	4.6	282± 8	5.2	224±5	5.8
2	0.000010	0.1	4.6	240± 9	4.8	210±5	5.8
3	0.000032	0.3	4.6	288±11	4.8	216±6	5.8
4	0.000100	1.0	4.6	212± 6	4.8	198±6	5.6
5	0.000316	3.4	4.6	206± 7	4.8	219±7	5.8
6	0.001000	10.8	4.6	205± 5	4.8	215±6	5.7
7	0.003160	34.0	4.6	150± 4	4.8	196±7	5.5

NO.	GRAM ATOMS OF BORON PER LITER	PPM. OF BORON	pH_1	RENEWED SOLUTIONS OF BORAX		UNRENEWED SOLUTIONS OF BORAX	
				Weight mgm.	pH_2	Weight mgm.	pH_2
8	0.000010	0.1	4.6	302± 6	5.2	197±5	5.8
9	0.000032	0.3	4.6	354± 9	5.2	198±5	5.8
10	0.000100	1.0	4.8	437±12	5.2	185±4	5.8
11	0.000316	3.4	4.9	473±15	5.3	173±3	5.8
12	0.001000	10.8	5.4	508±18	5.5	151±5	5.8
13	0.003160	34.0	5.9	407± 9	5.7	82±3	5.8

[a] Weight values represent an average obtained from the weights of twenty-five plants; they are followed by their probable errors.

The value pH_1 represents the initial pH of the solution.

The value pH_2 in the case of the renewed solutions refers to the pH at the end of one week and in the unrenewed solutions to the value at the end of nine weeks.

The boron concentrations were selected to include the optimum range previously demonstrated in the seedling experiments. One set of plants was grown in a boron-deficient medium in order to study the effect of a lack of boron on wheat, six cultures were supplied with boric acid, and six with borax. The boric acid and the borax solutions were made up so that corresponding cultures contained equal concentrations of boron. This series furnished experimental material for studying the effect of boron deficiency,

TABLE 9

Dry weights of the roots of wheat plants grown for nine weeks in renewed and unrenewed nutrient solutions containing varying quantities of boron supplied either as boric acid or borax.[a]

NO.	GRAM ATOMS OF BORON PER LITER	PPM. OF BORON	pH_1	RENEWED SOLUTIONS OF BORIC ACID		UNRENEWED SOLUTIONS OF BORIC ACID	
				Weight mgm.	pH_2	Weight mgm.	pH_2
1	None	0.0	4.6	21	5.2	25	5.8
2	0.000010	0.1	4.6	19	4.8	29	5.8
3	0.000032	0.3	4.6	28	4.8	26	5.8
4	0.000100	1.0	4.6	19	4.8	23	5.6
5	0.000316	3.4	4.6	16	4.8	25	5.8
6	0.001000	10.8	4.6	18	4.8	22	5.7
7	0.003160	34.0	4.6	13	4.8	15	5.5

NO.	GRAM ATOMS OF BORON PER LITER	PPM. OF BORON	pH_1	RENEWED SOLUTIONS OF BORAX		UNRENEWED SOLUTIONS OF BORAX	
				Weight mgm.	pH_2	Weight mgm.	pH_2
8	0.000010	0.1	4.6	32	5.2	24	5.8
9	0.000032	0.3	4.6	34	5.2	30	5.8
10	0.000100	1.0	4.8	46	5.2	35	5.8
11	0.000316	3.4	4.9	59	5.3	42	5.8
12	0.001000	10.8	5.4	50	5.5	38	5.8
13	0.003160	34.0	5.9	36	5.7	8	5.8

[a] The values represent one twenty-fifth of the total weight of the roots of twenty-five plants.

The value pH_1 refers to the initial pH of the solution.

The value pH_2 refers to the pH at the end of one week in the case of the renewed solutions, and nine weeks in the case of the unrenewed.

and the comparative stimulation effects of boric acid and borax. It also allowed a study to be made of the concentrations at which boric acid and borax began to be definitely toxic. By duplication of cultures, an additional series was prepared for the purpose of studying the effects of boron concentrations in unrenewed solutions as compared with the effects of the same concentrations in the primary series in which the solutions were renewed weekly, providing a supply of 7500 cc. of nutrient medium for 25 plants

every seven days. This experiment furnishes growth data for 650 plants grown in twenty-six different nutrient environments. The dry weights obtained from this series are listed in tables 8 and 9, and plotted in figures 3 and 4. The photographs of plates 1 and 2 show the condition of the plants one week before the termination of the experiment, and the final appearance of the plants is described in table 10.

TABLE 10

Condition of plants grown in various boron solutions, with respect to flower formation and tillering at the time of harvesting.[a]

BORIC ACID CULTURES

PPM. OF BORON	RENEWED SOLUTIONS			UNRENEWED SOLUTIONS		
	Flowers	Buds	Tillers	Flowers	Buds	Tillers
0.0	1	12	33	0	12	0
0.1	0	8	22	0	15	0
0.3	1	21	39	0	6	0
1.0	0	15	19	0	1	0
3.4	0	15	21	0	5	0
10.8	0	18	17	0	5	0
34.0	0	5	5	0	2	7

BORAX CULTURES

PPM. OF BORON	RENEWED SOLUTIONS			UNRENEWED SOLUUTIONS		
	Flowers	Buds	Tillers	Flowers	Buds	Tillers
0.0	1	12	33	0	12	0
0.1	1	20	32	0	0	0
0.3	1	23	40	0	5	0
1.0	9	16	37	0	0	0
3.4	10	14	34	0	0	0
10.8	14	10	23	0	0	0
34.0	0	19	11	0	0	1

[a] The term "flowers" in the above table refers to spikes completely emerged from the sheath, and the term "buds," to spikes formed and swollen, but still enclosed within the sheath.

Comparison of growth in renewed and unrenewed boron cultures. This study of the effect of renewal of solutions on the manifestation of boron effects is of particular significance. In the literature on boron, with the exception of the work by Warington (1923) and Collings (1927), no mention is made of the periodic and complete renewal of culture media. Sommer and Lipman (1926) and Johnston and Dore (1929) merely mention the renewal of the iron supply. McMurtrey (1929), in his work on the necessity of boron for tobacco, states that he did not renew his solutions "because frequent renewals tend to delay the manifestation of boron-deficiency symptoms."

The results of the experiment with renewed and unrenewed solutions bring out very clearly the discrepancies between data obtained by these two methods and the great desirability of renewing solutions in any attempt to discover the reactions of plants to known sets of solution conditions.

As early as the end of the first month there were marked differences in the condition of the plants in the two series, consisting chiefly of the rather pronounced chlorosis of the plants in the unrenewed series. This chlorosis was particularly advanced in the plants in those cultures supplied with un-

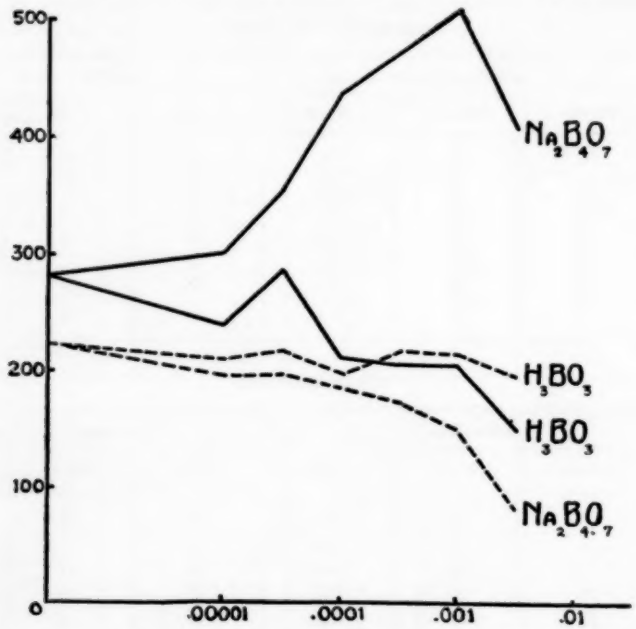

Fig. 3. Growth of tops of wheat plants grown in solutions containing borax and boric acid. Ordinates represent dry weights in milligrams. Abscissas represent gram atoms of boron per liter. Solid lines indicate renewed series and broken lines unrenewed series.

renewed solutions containing high concentrations of borax, and the difference between these cultures and their duplicates in the renewed series was particularly marked. It is possible that the chlorosis occurring in the unrenewed solutions was due in some part to iron deficiency, and that the greater depression of growth and increased chlorosis occurring in the high-borax cultures were caused by the further decrease in the availability of the iron due to reduced acidity. However, it is just as possible that these plants were equally affected by the lack of other nutrients, particularly in the highest borax concentration, where a visible, crystalline precipitate

lining the jar and encrusting the roots indicated that some nutrient material had been made unavailable to the plants. Premature tillering was observed at the end of the sixth week in both of the boron-deficient cultures, none occurring in any of the boron cultures until some time later. Even in this respect, however, a difference was observable between the renewed and unrenewed cultures, for in the unrenewed set every plant exhibited early tillering, whereas such tillers were present on only about one-half of the plants in the corresponding renewed solution. Moreover, in the case of the unrenewed set, these premature tillers died shortly after their formation, while those in the renewed culture grew normally.

Similarly an examination of the two sets of curves in figures 3 and 4 reveals the incompatibility of data obtained by these two methods. In the

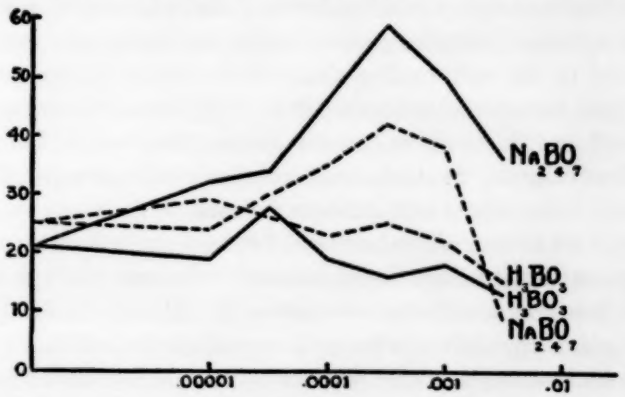

Fig. 4. Growth of roots of wheat plants grown in solutions containing borax and boric acid. Ordinates represent dry weights in milligrams. Abscissas represent gram atoms of boron per liter. Solid lines indicate renewed series and broken lines unrenewed series.

top growth, for instance, the curves indicate that borax produces greater dry weights than boric acid in the renewed cultures, whereas the reverse is true in the unrenewed solutions. This may be due to the fact that iron and other nutrients are less available in the borax cultures because of their lower acidity. Another striking difference is seen in the fact that those borax cultures which are most stimulating in the renewed series (3.4–34 ppm. of boron) exhibit the greatest toxicity in the unrenewed series.

The plants grown in the highest concentration of boric acid are also distinctly different in the two series. In both series, renewed and unrenewed, the dry weights of the plants indicate a decrease in growth as the margin of toxicity is approached. But in the renewed series this decrease in weight of the plants in the highest concentration of boric acid is shown

by the photographs of plate 1 to be accompanied by visible chlorosis and depression in growth, whereas in the unrenewed solutions the corresponding culture looks the best of the boric acid series. A similar discrepancy between the fresh weight or appearance of the plant and the dry weight has been described by Agulhon (1910) as characteristic of plants supplied with boric acid in amounts exceeding the optimum, and attributed to "over-mineralization." The photographs of the series (plates 1 and 2) emphasize the difference in the results obtained by renewed and unrenewed solutions, and the description of the condition of the plants when harvested (table 10) yields further confirmation from the aspects of vegetative development and maturity. In no case had a flower spike completely formed and emerged from the sheath in any of the unrenewed solutions. In the renewed solutions there was one case in the boron-deficient control, one case in the boric acid cultures and thirty-six cases in the borax solutions. If spikes still enclosed in the surrounding sheath be included in the estimation of flowering, the unrenewed cultures showed fifty-one cases compared with two hundred and thirty-three cases in the renewed series. The total number of normal tillers in the unrenewed series was eight, compared with three hundred and thirty-three in the renewed series.

Growth in the boron-deficient controls. In these control cultures great care was taken not to introduce boron into the solutions through any chance contamination. The water used was always freshly distilled before the cultures were made up, and the salts used were of the highest grade obtainable commercially. Johnston (1928) discussed the problem of the introduction of boron into nutrient solutions from glazed earthen-ware jars and Pyrex glassware. New glazed jars afforded enough boron to supply the needs of tomatoes, but after the jars had been used several times, the amount of boron that was leached out by the solution was insufficient to prevent the appearance of boron-deficiency symptoms. The jars used in the present experiment were well seasoned, having been previously used in culture experiments. There is, of course, the possibility of contamination through the use of Pyrex bottles in which the stock salt solutions were stored; but Sommer (1927) states that Pyrex, although a boro-silicate, does not yield sufficient boron for the normal growth of at least some plants.

The plants grown in the boron-deficient solutions exhibited none of the serious symptoms described in the literature by Sommer and Lipman (1926), Swanbeck (1927), McMurtrey (1929), Johnston and Dore (1929), and Johnston and Fisher (1930). One significant observation was that of premature tillering in the plants of the two boron-deficient cultures, and no others. Abnormal branching has been described as a boron-deficiency symptom by Sommer (1927), McMurtrey (1929), and Johnston and Dore

(1929), and is believed to be a response to a disturbance in the apical dominance of the plant due to typical degeneration of the apical meristem. In the renewed series the dry weights of roots and tops are lower in the boron-deficient control than in any of the borax cultures. On the other hand, they exceed the dry weights obtained in all the boric acid cultures with the exception of the solution containing 0.3 ppm. of boron. Similar relationships with regard to the formation of flowers are brought out by table 10. In the renewed series, about one-half of the plants in the boron-deficient solution are shown to have formed spikes. This proportion is exceeded by the cultures in the optimum range of boric acid concentrations (0.3–10.8 ppm.); but curiously enough this proportion is greater than that found for the first boric acid concentration—0.1 ppm. of boron as boric acid. The proportion of flowering in the boron-deficient culture is exceeded by all of the borax cultures; thus borax had as marked an effect on flower production as on dry yields.

It is apparent from the data of this experiment that the wheat plants were capable of developing for at least nine weeks, up to the flowering stage, in solutions to which no boron was added. If it is assumed, as seems justified from the work of Sommer and Lipman (1926) on a similar grain, barley, that minute quantities of boron are indispensable for the growth of wheat, it is evident that these traces of boron must have been present as impurities in the salts or that they were provided by solution of the culture vessels. The fact that the amounts of boron required by cereal grains is exceedingly small in comparison with those required by the Leguminosae is indicated by Warington (1923), Brenchley and Warington (1927), and Brenchley (1927), who found that wheat, barley, and rye came to full maturity in solutions supposedly free of boron. At least, these solutions did not contain enough boron to allow the full development of broad beans, scarlet runner, alfalfa, and crimson, white, and lesser clover.

Growth in boric acid cultures. Since this long-time experiment was undertaken with the primary purpose in view of determining whether there are differences in the effects of boric acid and borax on the growth of wheat plants, it is of interest to compare the results obtained with these two compounds, using the renewed solutions as a basis of study. An examination of figure 3 and table 8 indicates that when boric acid was added to the culture solutions here employed, it induced no significant stimulation of top growth, as indicated by dry weights. In one concentration (0.3 ppm. of boron), the top weights are very slightly higher than those of the control plants grown in the boron-deficient solution, but this difference does not exceed the range of possible error and so may not be significant. In every other boric acid concentration tested, the dry weights of the tops are lower

than those in the control culture. This failure to secure definite indications of stimulation above the control with boric acid solutions is interesting, in view of the fact that the control, according to the results of Sommer and Lipman (1926) with barley, should be considered subnormal because it is deprived of an element essential to growth. The superiority of the growth in the 0.3 ppm. solution is further suggested by the appearance of the plants, as shown in the photographs of plate 1 and by the figures and curves for the dry weights of roots (table 9 and figure 4). The figures for the dry weights of the roots are somewhat unsatisfactory, since the entire root mass of twenty-five plants was weighed as a single unit and the range of experimental error is unknown, and also because an error was introduced in the higher concentrations by the fact that crystals had precipitated upon the surface of the roots and could not be completely removed. However, the figures probably do suffice to show the general trend of growth.

In this experiment, as in those conducted with very young seedlings, there is considerable doubt as to whether evidence was obtained of a stimulating action of boric acid, under the conditions of these tests. Perhaps the one sign of any significant stimulation is found in table 10, which shows, in the case of the 0.3 ppm. solution alone, an increase in the number of flowers formed and a slight increase in the number of tillers. The curve for the boric acid cultures, with the one exception of the point representing the 0.3 ppm. yield, shows a gradual downward trend from the control, as the concentration of boric acid is increased. The highest boric acid concentration (34 ppm. of boron) exerted a definitely toxic effect, as shown by the drops in the curves for root and top growth, and by the photograph of this culture (number 7) in plate 1. This result is in keeping with data obtained in the young seedling experiments which indicate that a solution containing 34 ppm. of boron is within the toxic range.

Growth in borax cultures. The curves for the growth in the renewed solutions of borax and the photographs of the plants grown in these cultures (plate 2) leave little doubt as to the stimulation resulting from the addition of borax in concentrations varying from 1 to 34 parts per million of boron to the basic solution employed in this experiment. A study of the curves in figures 3 and 4 shows that there is an increase in dry weight with increasing concentrations of borax up to an optimum concentration supplying 10.8 ppm. of boron. In this solution the top growth, as evidenced by dry weight, is almost twice as great as that in the control, and the root growth almost three times as great. Above this point an increase in the concentration of boron is accompanied by a decrease in dry yield, as the optimum is passed and the range of toxicity is entered. The highest borax concentration used, providing 34 ppm. of boron, although it is definitely

above the optimum for growth, nevertheless permits the development of healthy, green tops, as well as greater dry weight and a higher proportion of flowering than the control. In the renewed borax cultures (table 10) it was found that there is an increase in the number of completely opened spikes which is correlated with increasing borax concentration until the 10.8 ppm. concentration is passed. This luxuriant growth in the high borax cultures is surprising in that the concentrations used exceed those commonly thought of as optimal or even safe.

Even more surprising, perhaps, than the relatively low toxicity of borax is the difference between the results obtained in the borax cultures and those obtained in the corresponding boric acid cultures containing equivalent gram-atomic concentrations of boron. This difference closely parallels the results based on the root elongation of very young seedlings studied in the previous experiments, but it is surprising nevertheless. In the first place, the optimum concentrations of boric acid and borax are entirely different. In the boric acid curve, with the exception of the point for the 0.3 ppm. concentration, there is a general downward trend. In the borax curve, there is a pronounced rise toward the optimum concentration of 10.8 ppm., with depression in the higher concentration. In none of the renewed boric acid cultures, with the exception of the apparently optimum concentration, does the growth equal or exceed that of the control, whereas in the borax cultures every tested concentration, including the one which supplies only 0.1 ppm. of boron, produces better growth than that in the control solution. Agulhon (1910) reported that boric acid solutions containing 2.5 to 10 ppm. of boron were stimulating to wheat grown in sterile cultures, but that higher concentrations decreased growth, the concentration of 20 ppm. being definitely toxic. These figures do not agree with the data for boric acid found in the present study. Stimulation here occurs at 0.3 ppm., if at all, and all concentrations above this result in a depression of growth. Agulhon's figures do, however, bear some resemblance to the results here obtained with the borax cultures.

The results of the long-time experiment bear out the preliminary findings in the seedling experiments, indicating that there is a marked difference between the stimulating effects of the alkaline and acid borates on the growth of wheat. Unlike boron toxicity, which for a given plant is a fairly constant function of the boron concentration and is not greatly altered by the nutrient balance or the reaction of the solution, the stimulation effects observed in these experiments with wheat seem to be conditioned by the hydrogen-ion concentration of the medium. It seems reasonable to discard the possibility that the sodium ion in itself is responsible for the stimulation found in the borax cultures, because in the experiments with

young seedlings it was found that the neutral sodium chloride failed to produce the stimulation which was produced by the alkaline sodium salts, the borate, carbonate, and bicarbonate. Duggar (1920) reported that nutrient solutions with higher pH values than those commonly obtained with high concentrations of the acid phosphates were favorable to wheat plants, particularly when grown under conditions inducing high transpiration rates. An examination of the pH values for the solutions (table 8) used in the long-time experiment shows that the boric acid and boron-deficient solutions all had an initial pH value of 4.6, and that the borax solutions ranged from 4.6 to 5.9. By the time for solution renewal at the end of the first week, the boron-deficient solutions had shifted to 5.2, all of the boric acid cultures to 4.8, and the borax solutions to values varying from 5.2 to 5.7. These differences in pH values are apparently correlated with the superiority in growth of the borax and boron-deficient cultures over the majority of the boric acid cultures.

Two possibilities are suggested by these results. The differences between the results in the boric acid and borax cultures may indicate that the hydrogen-ion concentration serves as a sort of limiting factor for boron stimulation in wheat, or that the alkalinity of the borax in itself may be the causal factor in this stimulation. If the latter supposition is true, it appears that a frequently renewed culture solution having a pH value of 5.5 is far superior for the growth of wheat to a similar solution having a pH value of 4.8.

TABLE 11

The growth of wheat roots in nutrient solutions, the pH values of which were varied by using different proportions of monobasic and dibasic potassium phosphate.[a]

KH_2PO_4, cc. IN 1100 cc.	K_2HPO_4, cc. IN 1100 cc.	pH	GROWTH		
			1A mm.	1B mm.	Ave. mm.
44.0	0.0	4.4	90	84	87
41.8	2.2	5.0	95	97	96
39.6	4.4	5.4	95	95	95
35.2	8.8	5.8	89	92	91
31.8	13.2	6.0[b]	85	83	84

[a] Each solution contained 0.02 m calcium nitrate, 0.02 m magnesium sulphate, and 0.02 m potassium phosphate.

The distilled water values were 77 and 82 mm., the average being 80 mm.

[b] Slight precipitation of calcium or magnesium occurred in this solution.

Some indication that the remarkable difference between the boric acid and borax series is primarily due to the difference in the hydrogen-ion concentration may be obtained from a subsequent test that was made with

very young wheat seedlings. Nutrient solutions were used which contained 0.02 m calcium nitrate and 0.02 m magnesium sulphate, and varying proportions of 0.02 m acid potassium phosphate and 0.02 m dibasic potassium phosphate. This series afforded a pH range from 4.4 to 6.0, and the results (table 11) indicate a slight increase in growth in the cultures with pH values between 5.0 and 5.8. The results for this experiment add further weight to the supposition that lower hydrogen-ion concentration in itself may be the important factor. Further work would be necessary, however, using solutions in which the boron factor is kept constant, and at a minimum, and the hydrogen-ion concentration varied, in order to prove definitely that the alkalinity of these borax solutions is the sole factor responsible for the remarkable stimulating effect they exert on wheat.

SUMMARY

The following conclusions are derived from observations made on the root growth of wheat seedlings supplied with boron solutions during a period of four days following germination, and also on the development of wheat plants in nutrient solutions over a period of nine weeks:

The degree of the toxicity of boron compounds depended on the concentration of the boron in the solution. Potassium borate, sodium borate, and boric acid exhibited similar toxicity when the boron concentrations which they afforded were equivalent.

A concentration of approximately 50 ppm. of boron caused a retardation of 40 per cent in the growth of wheat, and a concentration of 100 ppm. inhibited growth almost completely.

The toxicity of boron was the same whether the element was supplied to the plants in the form of a single-salt solution or as a component in a balanced nutrient medium.

No antagonism was evident between boron and either calcium or iron.

An optimum range of concentrations of sodium borate and potassium borate lay between 3 and 20 ppm. of boron. These alkaline borates were distinctly stimulating to the root growth of young seedlings, and to the development of plants grown for nine weeks (to the flowering stage). The optimum concentration of each salt corresponded to about 10.8 ppm. of boron.

Solutions of boric acid, on the other hand, did not stimulate the growth of the roots of very young seedlings. A slight stimulating effect, as evidenced by dry weights and flower development of the mature plants, was noted only in the boric acid solution containing 0.3 ppm. of boron.

From the results obtained with very young wheat seedlings grown in solutions of alkaline and neutral sodium salts, and in nutrient solutions in

which the hydrogen-ion concentration was varied by altering the proportions of monobasic and dibasic potassium phosphate, it is apparent that alkalinity was an important factor in the stimulation of these seedlings. The results of the experiment of long duration indicate a similar superiority of lowered hydrogen-ion concentration for wheat plants grown to the flowering stage. The difference between the growth in optimum concentrations of the alkaline borates and equivalent concentrations of boric acid may be due either to the fact that the low hydrogen-ion concentrations of the potassium and sodium borates is the direct cause of stimulation, or that the hydrogen-ion concentration of the culture medium serves as a limiting factor determining the extent to which boron stimulation may manifest itself. Most of the evidence secured in this study seems to favor the former alternative.

The results with initially identical renewed and unrenewed solutions were so incompatible as to render questionable many of the data on boron published from results obtained with unrenewed solutions.

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Description of plates

The photographs of plates 1 and 2 show cultures of wheat plants at the end of eight weeks of growth in nutrient solutions supplied with varying amounts of boron in the form of boric acid and borax. The basic nutrient solution contained 0.01 m KH_2PO_4, 0.005 m $MgSO_4$, 0.005 m $CaNO_3$, and 0.00001 m $FeSO_4$. See tables 8, 9, and 10.

PLATE 1

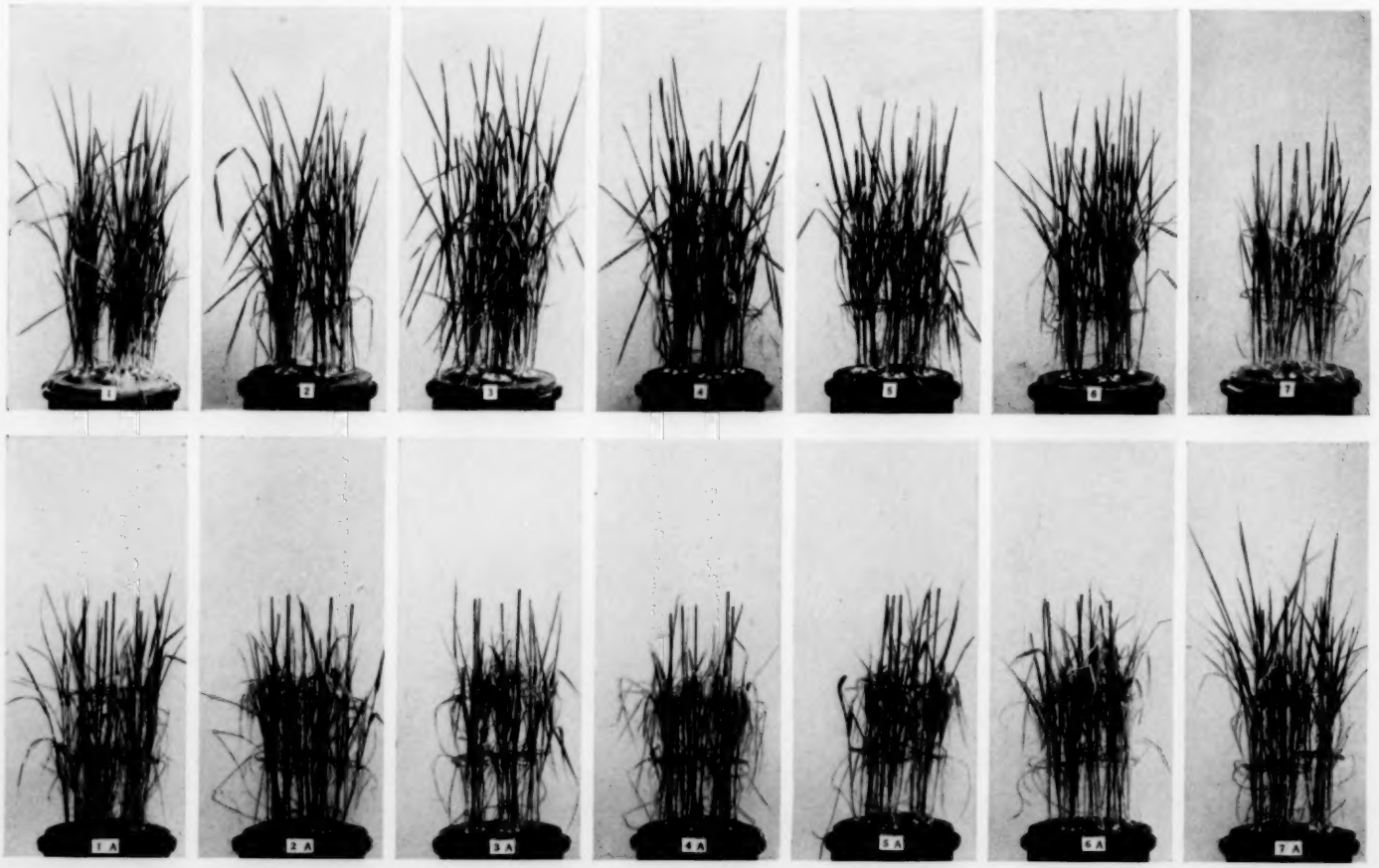
BORIC ACID CULTURES

Cultures 1 to 7 were grown in renewed solutions, and cultures 1A to 7A were grown in unrenewed solutions. Cultures 1 and 1A are the boron-deficient controls for these two series. Cultures 2 to 7 and 2A to 7A represent boric acid concentrations providing 0.1 to 34 ppm. of boron. In the renewed series, the best growth is shown in culture 3 supplied with 0.3 ppm. of boron. Culture 7 shows boron toxicity. In the unrenewed series all the cultures are somewhat chlorotic.

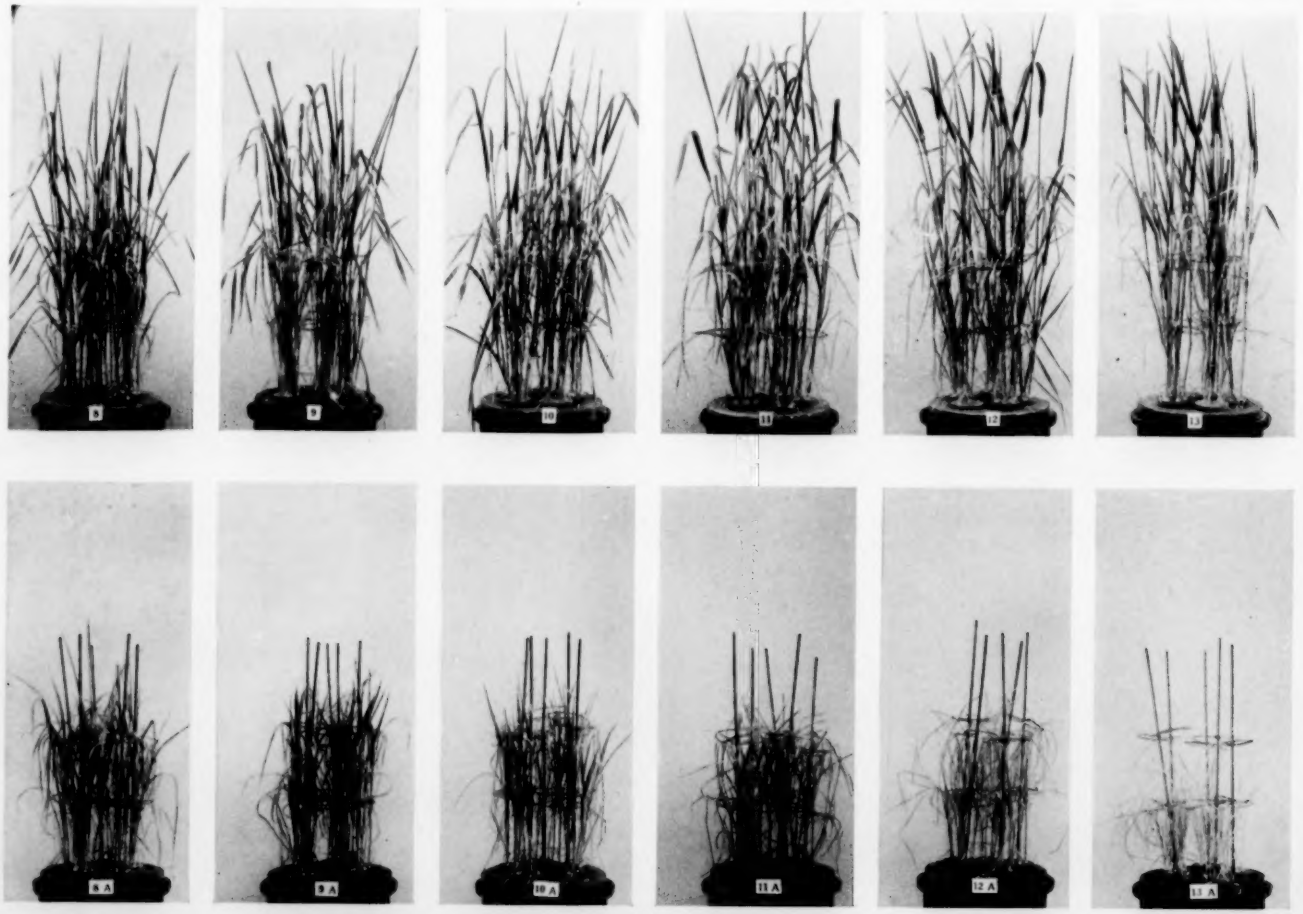
PLATE 2

BORAX CULTURES

These cultures were grown in solutions of borax providing from 0.1 ppm. of boron (cultures 8 and 8A) to 34 ppm. (cultures 13 and 13A). Cultures 8 to 13, in which the solutions were renewed weekly, exhibit marked stimulation. Corresponding cultures 8A to 13A, in which solutions were unrenewed, exhibit marked chlorosis and depression in growth. For the degree of stimulation or depression, see control culture 1 in plate 1.



MORRIS: EFFECTS OF BORON ON WHEAT



MORRIS: EFFECTS OF BORON ON WHEAT

A review of the American species of Daltonia

EDWIN B. BARTRAM

(WITH PLATES 3, 4)

The genus *Daltonia* was established by Hooker and Taylor in memory of their friend, the Rev. James Dalton, Rector of Croft, in Yorkshire, whose keen interest in botany and bryology is reflected by a number of noteworthy discoveries of rare mosses and flowering plants from this district.

Curiously enough the type species, *D. splachnoides* (Sm.) Hook. & Tayl., is isolated in a few scattered localities in Ireland, while elsewhere the group is almost entirely confined to elevated tropical regions. In America the center of distribution seems to be in Cordilleran regions of Colombia and Ecuador, with extensions northward to Mexico and the West Indies, eastward to southeastern Brazil and southward to Bolivia and Chile. The reported occurrence of *D. splachnoides* in Mexico and the Antilles is probably the result of a rather hazy understanding of the type species and its American associates. *D. gracilis*, one of the most widely distributed of the American species, is undoubtedly very close to *D. splachnoides*, but the European plant should be, and I think is, clearly separable through the more incrassate upper leaf cells, the stronger, more cartilaginous border, shorter leaves, and reduced size throughout: at least no transitional forms with clearly correlated characters have been observed in any of the American collections that would tend to narrow the gap.

With a few notable exceptions the American species are closely interrelated and naturally fall into several well marked groups. No obvious distinctions have been found in either the perigonial or perichaetial leaves, the peristome, lid or calyptra, all of which seem to be fairly constant throughout the genus. Unfortunately the vegetative characters, which have been extensively relied upon to differentiate the species, are rather unstable, and although there are undoubtedly reasonable limits within which these variations can be accommodated, the question of establishing these limits and of evaluating the distinctions has often proved a delicate and tedious one.

Four species are obviously distinct: *D. macrotheca* by the elongated, almost filiform stems with distantly imbricated leaves; *D. Jamesoni* by the large, pellucid quadrate leaf cells and almost percurrent costa: *D. latolimbata* by the rounded, incrassate upper leaf cells and the band of long, narrow juxta-costal cells extending from mid-leaf to the insertion; and *D. brevinervis* by the linear, incrassate upper leaf cells extending in a central

wedge-shaped band to the insertion. Of the remaining species, one group, comprising *D. longifolia*, *D. pulvinata*, *D. braziliensis*, *D. aristata*, and *D. androgyna*, may be defined by the essentially flat leaf margins and rounded leaf cells. In this group the lamina is occasionally broadly reflexed here and there and very rarely narrowly recurved, but never regularly and consistently revolute as in all but one or two of the remaining species. The leaves of *D. stenophylla* and *D. gracilis* are sometimes nearly plane, but their smaller size and angular or elongated areolation easily distinguish them from those of *D. longifolia* and its allies, in which the leaf cells are oval and rounded.

Mitten's key, based on the leaf outline, is helpful as far as it goes; the treatment by Brotherus in both editions of Engler and Prantl by subdivisions into arbitrary groups does not do much to clarify the situation. It was at the friendly suggestion of Mrs. Britton, (who had already made a chronological list of all the American species and studied the West Indian collections) and also by means of the loan of the types not represented in the herbarium of the New York Botanical Garden, that this revision was undertaken. All the Antillean specimens and their manuscript names have been referred to South American species. Needless to say this study would have been utterly impracticable without the use of the collections which Mrs. Britton so graciously placed at my disposal. Dr. Herzog has very generously loaned his Bolivian collections, including the types of several species, together with several Brazilian specimens and a limited but highly interesting series of unnamed collections from Colombia and Bolivia, all of which have been incorporated in the present study. Through the kindness of Dr. Reimers it has been possible to examine portions of the Mueller types which rest in the Botanical Museum at Berlin-Dahlem and Dr. Lindberg has very kindly loaned type material of several South American species from the Brotherus herbarium. Such friendly coöperation is deeply appreciated and leaves a lasting sense of gratitude.

KEY TO SPECIES

Leaf margin flat

Upper leaf cells short, oval-rhomboidal, 1:2 or less, seta stout, propagulae present. . 1. *D. pulvinata*

Upper leaf cells oval, 1:3 or more, often more or less pitted, seta slender, propagulae wanting

Leaves oblong-ligulate, up to 3.5 mm. long. . . . . 2. *D. longifolia*

Leaves lanceolate, 2.5–3 mm. long

Areolation dense, upper cells up to $7 \times 18\mu$, border wide

Seta 6–12 mm. long. . . . . 3. *D. braziliensis*

Seta 4–5 mm. long. . . . . 4. *D. aristata*

Areolation lax, upper cells up to $10 \times 30\mu$, border narrow . . . . 5. *D. androgyna*

Leaf margin revolute
Leaves laxly imbricated, stems slender and elongated.....6. *D. macrotheca*
Leaves densely imbricated, stems shorter
Costa ending about mid-leaf, upper cells linear.....7. *D. brevinervis*
Costa ending ¾ or more up, upper cells not linear
Leaves ovate, costa nearly percurrent.....8. *D. Jamesoni*
Leaves lanceolate, costa shorter
Basal leaf cells linear, firm, border indistinct below
Leaves lanceolate, 0.4–0.5 mm. wide, propagulae present....9. *D. Lindigiana*
Leaves linear-lanceolate, 0.3 mm. wide or less, propagulae usually wanting
10. *D. stenophylla*
Basal cells oblong, border distinct to insertion
Robust plants, leaves 3–4 mm. long, border wide
Seta smooth
Border 10–15 rows wide at base.....11. *D. bilimbata*
Border 7–9 rows wide at base.....12. *D. pellucida*
Seta rough above
Juxta-costal basal cells not differentiated.....13. *D. peruviana*
Juxta-costal basal cells long linear, similar to border cells.....
14. *D. latolimbata*
Slender plants, leaves less than 3 mm. long, border narrow
Seta smooth
Leaves oblong-ligulate, basal cells short oblong, firm and pellucid.....
15. *D. trachydontia*
Leaves linear-lanceolate, basal cells linear-oblong, delicate and hyaline.....16. *D. tenuifolia*
Seta rough above
Leaves linear-lanceolate, basal cells up to 50μ long, linear-oblong....
17. *D. gracilis*
Leaves lanceolate, basal cells 35μ or less long, oblong....18. *D. ovalis*

1. DALTONIA PULVINATA Mitt. Jour. Linn. Soc. Bot. **12**: 398. 1869.

Autoicous. Plants densely tufted, yellowish green, glolsy. Stems up to 1.5 cm. high, simple, about 2 mm. wide with leaves, radiculose at base, with clusters of spindle shaped, septate propagulae in the leaf axils. Leaves densely imbricated, erect spreading, spirally contorted when dry, flexuose when moist, carinate with a broad median fold, oblong-ligulate, sharply acuminate, 2.5 to 3 mm. long by 0.6 mm. wide at base, margin flat, often broadly reflexed toward base but not revolute, entire or very minutely denticulate at apex, border pellucid, sharply defined, 7–10 rows wide at base, 3–4 rows at mid-leaf and 2 rows at apex; costa ending about 4/5 up, 35μ wide at base, channelled; cells of apical blade short, oval-rhomboidal, 6–8μ wide by 12–14μ long, hardly incrassate, median cells similar, basal cells short-rectangular, hyaline. Seta

stout, scarcely twisted, 5–6 mm. long, reddish, scabrous above; capsule erect, short oval, 1 mm. high by 0.7 mm. broad, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose; lid erect, rostrate; calyptra slightly scabrous above, copiously fringed, spores minutely roughened, 22–25μ in diameter.

Type Locality: Andes Bogotenses, near Bogota, Colombia.

Distribution: Colombia, Ecuador, Bolivia.

Material seen: COLOMBIA: Andes Bogotenses, prope Bogota, *Weir* (type); on branches of stunted trees by the way from Tipiguira to Pacho, 8000 ft., *Weir* (propagulae abundant).—ECUADOR: Guayrapata ad ramulos, *Spruce* (No. 566?).—BOLIVIA: Incacorral, alt. 2200 m., *Herzog 4950* in part.

Remarks: This species closely resembles both *D. longifolia* and *D. braziliensis* but appears to be distinct in the shorter, less incrassate leaf cells, the stout, short seta and larger spores. The occurrence of axillary propagulae may also be a distinctive feature. They have been found in all the specimens studied, and are especially abundant in the specimens from near Pacho, Colombia.

2. DALTONIA LONGIFOLIA Tayl. Lond. Jour. Bot. **7**: 284. 1848.

D. crispata Schimper ex Besch. Mem. Soc. Sci. Cherbourg **16**: 228. 1872. *D. robusta* Ångstr. Öfvers. K. Vet. Akad. Foerhand. **1873**[5]: 117. 1873. *D. Dussii* Broth. Symb. Ant. **3**: 426. 1903.

Autoicous. Plants in rather lax tufts, yellowish green, glossy. Stems up to 2.5 cm. high, simple or sparingly branched, 2–3 mm. wide with leaves, radiculose below. Leaves closely imbricated, erect spreading and rather spirally contorted when dry, flexuose when moist, carinate with a broad median fold, oblong-ligulate, sharply acuminate, 3 to 3.5 mm. long by 0.6 mm. wide at base; margin flat, minutely denticulate toward apex; border pellucid, sharply defined, 8–15 rows wide at base, about 4 rows at mid-leaf and 2 rows at apex; costa ending about 4/5 up, 45μ wide at base, channelled; cells of apical blade oval-oblong, 6–7μ wide by 15–25μ long, median cells similar, often arranged in oblique rows, basal cells narrowly oval to linear-rhomboidal, rather incrassate and pellucid and often lightly pitted. Seta slender, twisted to left when dry, up to 10 or 12 mm. long, reddish, scabrous above; capsule erect, oval-cylindrical, up to 1.5 mm. long by 0.8 mm. wide, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose; lid erect, rostrate, about 1 mm. long, yellowish; calyptra slightly scabrous above, copiously fringed; spores minutely roughened, 12–15μ in diameter.

Type Locality: Mt. Pichincha near Quito, Ecuador.

Distribution: Mexico, Guatemala, Haiti, Martinique, Colombia, Ecuador, Galapagos Islands, Bolivia.

Material seen: MEXICO: Huatusco, Vera Cruz, *Liebmann;* on oaks, Honey Station, Hidalgo, *Pringle 10487*.—GUATEMALA: Alta Verapaz, Cubilguitz, *Turckheim 6660*,

6661; Alta Verapaz, prope Coban, *Turckheim 6662.*—HAITI: vicinity of Furcy, *Leonard 4620b.*—MARTINIQUE: Ajoupa Bouillon, *Pere Duss 345.*—COLOMBIA: Magana, Cordillera Central, *Killip & Hazen 12092a.*—ECUADOR: Pichincha near Quito, *Jameson* (type); Autombos, *Spruce 565;* Tunguragua, *Spruce.*—GALAPAGOS ISLANDS: Chaves Island, *N. J. Anderson;* James Island, *Alban Stewart 6046a.*—BOLIVIA: Rio Pelichucho, *R. S. Williams 2751;* Santa Barbara, *R. S. Williams 1816;* Talschlucht von Tablas, *Herzog 4650;* Bergwald von Tocorani, *Herzog 4040, 4081d* in part; auf Baumasten beim Sillar, *Herzog 2696a*; Incacorral, *Herzog 5091a* in part.

Remarks: I have endeavored in all fairness to find some characters that might distinguish the various collections comprised in the synonymy of this species, but without success. *D. longifolia* is apparently an unstable type, but the variations are only relative, and may be included in the outline of a conservative specific concept. Indeed *D. pulvinata*, *D. longifolia*, *D. brazilinensis*, *D. androgyna*, and *D. aristata* form a very closely united group well defined from the other species by the essentially flat leaf margins and rounded leaf cells but not distinguished from each other by any salient characters. From a radical viewpoint the entire group might be subordinated to *D. longifolia*, but as this might tend to obscure rather than clarify our understanding of the elements involved, I have followed a middle course and tried to group the plants according to their natural affinities and geographical distribution, not, however, without considerable mental reservation. The leaf margins in the plants comprising this group are essentially flat, but occasionally the lamina is broadly reflexed, and very rarely narrowly recurved, but never consistently enough to be confused with the much larger group of species in which the margin is usually plainly and narrowly revolute.

3. DALTONIA BRAZILIENSIS Mitt. Jour. Linn. Soc. Bot. **12:** 399. 1869.

D. leucoloma Hampe, Vidensk, Medd. Nat. Foren. Kjöb. **1874:** 152. 1875.

Autoicous. Plants fulvous green, glossy. Stems up to 1.2 cm. high, more or less branched, 2–3 mm. wide with leaves, radiculose below. Leaves closely imbricated, erect and slightly spirally contorted when dry, flexuose when moist; carinate with a median fold, lanceolate, sharply acuminate, 2.5 mm. long by 0.6 mm. wide at base; margin flat, entire or very minutely denticulate above; border yellowish pellucid, 7–14 rows wide at base, about 4 rows at mid-leaf and 2 rows above; costa ending about 2/3 up, 45μ wide at base, channelled; cells of apical blade oval-rhomboidal, 6–7μ broad by 14–18μ long, median cells similar often oblique, basal cells rectangular and rhomboidal, all slightly incrassate. Seta slender, 6–12 mm. long, reddish, scabrous above; capsule erect, oval, up to 1.5 mm. high by 0.8 mm. broad, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose, teeth strongly trabeculate on inner side; lid erect, about 1 mm. long, yellowish; calyptra slightly scabrous above, fringed; spores minutely roughened, 14–18μ in diameter.

Type Locality: Province of Minas Geraes, Brazil.

Distribution: Brazil.

Material seen: Sierra de Piedade, Minas Geraes, Brazil, *Gardner 78* (type); woods near Corritaba, *Weir;* Rio, *Glaziou 5820;* Rio Janeiro, *Glaziou 5620.*

Remarks: Leaves from the type collection of *D. braziliensis* show a variable border from 5 to 12 rows wide at the base while those from the type collection of *D. leucoloma* show a border from 7 to 14 rows wide at the base. The setae in *D. leucoloma* are rather shorter, but neither of these characters appear to be stable enough to warrant a specific distinction.

4. DALTONIA ARISTATA Geheeb & Hampe, Vidensk. Meddel. Kjøb. **1879–80:** 121. 1879.

D. Uleana C. Müll. Bull. Herb. Boiss. **6:** 111. 1898.

Autoicous and synoicous. Plants loosely tufted, yellowish green, glossy. Stems up to 1.5 cm. high, simple or branched, about 3 mm. wide with leaves, radiculose below. Leaves erect spreading, flexuose and lightly twisted when dry, flexuose when moist, ovate-lanceolate, sharply acuminate, up to 2.75 mm. long by 0.7 mm. wide at base; margin flat, entire or minutely denticulate above; border pellucid, 7 to 10 rows wide at base, 4–6 rows wide at mid-leaf and 1 or 2 rows wide above; costa ending about $\frac{3}{4}$ up, 45μ wide at base, channelled; cells of apical blade oval-rhomboidal, 6–7μ wide by 16–18μ long, median cells similar and often obliquely arranged on one side, basal cells oblong and rhomboidal, all slightly incrassate. Seta short, 4–5 mm. long, reddish, scabrous above; capsule short oval, erect, about 0.6 mm. high by 0.5 mm. wide, exothecal cells strongly collenchymatous; peristome not seen; lid conic subulate, yellowish (ex desc.); spores unknown.

Type: Prope Apiahy, San Paulo, Brazil.

Distribution: Endemic.

Material seen: BRAZIL: prope Apiahy, San Paulo, *Puiggari* (type); Catharina, Serra Geral, *E. Ule 865.*

Remarks: There is little beyond the shorter setae to separate these plants from *D. braziliensis,* and I am very doubtful if they represent anything more than a form of this species.

5. DALTONIA ANDROGYNA Geheeb & Hampe Flora **64:** 405. 1881.

Autoicous. Plants yellowish green, glossy. Stems up to 1 cm. high, simple, about 2 mm. wide with leaves, radiculose below. Leaves closely imbricated, erect and lightly spirally contorted when dry, flexuose when moist, carinate with a median fold, ovate-lanceolate, sharply acuminate, 2.5 mm. long by 0.6 mm. wide at base, margin flat, entire or very minutely denticulate above; border pellucid, 4–5 rows wide at base, about 3 rows wide at mid-leaf and 1–2 rows wide above; costa ending about 2/3 up, 40μ wide at base, channelled; cells of apical blade oblong-rhomboidal, up to 10μ wide by 20–30μ long, median

cells similar, basal cells oblong and rhomboidal becoming narrower toward costa, all rather incrassate and slightly pitted. Seta slender, about 10 mm. long, reddish, very scabrous above and rough half way down; capsule erect or inclined, oval, 1.5 mm. high by 0.9 mm. wide, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose; lid erect, 0.65 mm. high, yellowish; spores minutely roughened, 15–17μ in diameter.

Type Locality: prope Apiahy, San Paulo, Brazil.
Distribution: Endemic.
Material seen: Brazil: prope Apiahy, San Paulo, *Puiggari 985b* (type).

Remarks: This plant appears to be distinct from *D. braziliensis* in the larger, pitted leaf cells and the narrower border and from *D. aristata* by the longer seta, larger areolation and narrower border.

6. DALTONIA MACROTHECA Mitt. Jour. Linn. Soc. Bot. **12**: 402. 1869.

Autoicous. Plants pale, yellowish green, slightly glossy. Stems dark red, up to 4 cm. long, slender and flexuous, simple, about 1 mm. wide with leaves, radiculose at extreme base. Leaves laxly imbricated, erect, flexuose and slightly twisted when dry, erect spreading and flexuose when moist, carinate with a median fold, narrowly lanceolate, long and slenderly acuminate, 2.5 mm. long by 0.5 mm. wide at base; margin narrowly revolute on one or both sides from base nearly to apex, usually flat for a short distance below point, entire; border pellucid, 7–9 rows wide at base, 4–5 rows wide at mid-leaf and 2–3 rows wide above, confluent at apex, sharply defined below; costa ending about 2/3 up, 40μ wide at base, channelled; cells of apical blade oval-rhomboidal, up to 7μ wide by 20–28μ long, median cells similar, basal cells rectangular and rhomboidal, rather lax, all lightly incrassate. Seta slender, 12–14 mm. long, dark red, scabrous above; capsule inclined, oval-cylindrical, 2.1 mm. long by 1 mm. wide, dark brown; peristome yellowish, densely papillose, the teeth with several narrow slits along the median line; lid not seen; calyptra smooth above, copiously fringed; spores slightly rough, 10–12μ in diameter.

Type Locality: Chimborazo, Ecuador.
Distribution: Endemic.
Material seen: Ecuador: cinchona forest, Chimborazo, *Spruce* (type)

Remarks: The slender, elongated stems, laxly imbricated leaves and large capsule characterize this species clearly. It is easily segregated from *Lepidopilum chloroneuron*, with which it is entangled in the type collection, by the dark red, almost black stems, and the erect flexuose narrow leaves.

7. **Daltonia brevinervis** sp. nov.

Autoicous, male flowers about 0.7 mm. long, of 5 or 6 ovate, acute, entire perigonial bracts, the inner ecostate, the outer faintly nerved in the lower half, enclosing 2 or 3 antheridia without paraphyses. Plants in rather lax tufts, pale

green and glossy at the tips, brown below. Stems robust, up to 3 cm. long, simple or fasiculately branched, about 2 mm. wide with leaves, radiculose toward the base and often denuded of leaves in the older parts. Leaves closely imbricate, erect appressed and straight when dry, erect spreading when moist, carinate-concave without a median fold, oblong-ligulate, acute, 2 mm. long by 0.5 mm. wide at base; margin narrowly revolute from just below apex to insertion, entire; border yellowish pellucid, sharply defined at base, merging with the lamina cells about 1/3 up and indistinct above, 6–8 rows wide at base; costa slender, flat and indistinct, about 30μ wide at base, blending with the elongated lamina cells about mid-leaf; cells of apical blade linear, about 5μ wide by 40–50μ long, yellowish pellucid and rather obscure, slightly incrassate, shorter toward the margins and extreme apex, median cells similar and extending in a V shaped band to the base of the costa, basal cells between the median band and margin oval and short rectangular with rounded ends, 6–8μ wide by 12–24μ long, pellucid to hyaline. Seta slender, about 12 mm. long, usually scabrous throughout; capsule erect or slightly inclined, short oval, about 1 mm. high by 0.8 mm. wide, dark brown; peristome yellowish, densely papillose (fruit all old); lid not seen; calyptra conical, smooth above, copiously fringed; spores roughened, about 15μ in diameter.

Type: an der Rinde von Vorpostenbaumchen, Paramo El Boqueron near Bogota, Colombia, 3300 meters, *K. Troll 2176* in 1929. Com. Herzog.

Distribution: Known only from the type locality.

Remarks: This very interesting species was received from Dr. Herzog with other specimens of *Daltonia* from the same region. It seems to have no close affinity with any other known species, and is unique in the short nerve and linear areolation of the upper lamina, which converges in a wedge-shaped band to the base of the nerve. The area of short, hyaline cells between this band and the border is clearly differentiated, and ends above in a somewhat acute angle near the border. The type is deposited in the herbarium of the writer.

8. DALTONIA JAMESONI Tayl. Lond. Jour. Bot. **7**: 283. 1848.

Autoicous. Plants in compact tufts, yellow, slightly glossy. Stems robust, stiffly erect, up to 5 cm. long, simple or with few erect branches, about 1 mm. wide with leaves, densely radiculose and matted rogether in lower parts. Leaves closely imbricated, appressed and lightly twisted when dry, closely appressed with flexuose tips when moist, carinate with a broad median fold, broadly ovate, sharply acuminate, 2 mm. long by 0.8 mm. wide, margin narrowly revolte, entire; border yellowish pellucid, narrow, sharply defined, 3–5 rows wide at base, about 3 rows at mid-leaf and 2 rows wide above; costa faint, usually obscured by the median fold, about 30μ wide at base, flat, ending in acumen just below point; upper and median leaf cells quadrate and short rectangular, pellucid, somewhat incrassate, about 15μ wide by 15–25μ long,

basal cells more elongate up to 50μ long. Seta dark red, 8–12 mm. long, scabrous above; capsule erect, oval-cylindrical, 1.4 mm. high by 0.5 mm. wide, dark red, exothecal cells strongly collenchymatous; peristome pale yellow, densely papillose; lid erect, rostrate, 1 mm. long, yellowish; calyptra scabrous above, copiously ciliate; spores roughened, 20–25μ in diameter.

D. JAMESONI var. LAEVIS Herzog, Bibl. Bot. 87: 128. 1926.

Distinguished from the type by the seta almost smooth throughout.

Type Locality: Ecuador, Mt. Pichincha.

Distribution: Ecuador, Bolivia (var.).

Material seen: ECUADOR: summit of Mt. Pichincha on hillocks of Bolax *Jameson* in 1847 (type).—BOLIVIA: an feuchten felsen der Cerros de Malaga, ca. 4000 m., *Herzog 4415* (var.).

Remarks: The broad leaves, large subquadrate, pellucid leaf cells and almost percurrent costa separate this plant unmistakably from any of its associates.

9. DALTONIA LINDIGIANA Hampe, Ann. Sci. Nat. Bot. V. **4**: 363. 1866.

D. irrorata Mitt. Jour. Linn. Soc. Bot. **12**: 399. 1869. *D. Stewartii* R. S. Williams, Bryologist **27**: 38. 1924.

Autoicous. Plants in rather compact tufts, golden brown, glossy. Stems usually robust, erect or ascending, up to 3 cm. long, usually branched, about 2 mm. wide with leaves, sparingly radiculose below, with axillary, spindle shaped, septate propagulae. Leaves closely imbricated, erect and straight or slightly flexuose when dry, erect-spreading when moist, carinate with a median fold, narrowly lanceolate, acuminate, up to 4 mm. long by 0.5 mm. wide at base; margin narrowly revolute on one or both sides, entire; border pellucid, rather indistinct, blending with the elongated basal cells below, 8–10 rows wide at base, 4–5 rows wide at mid-leaf and 1–2 rows wide above; costa about 40μ wide at base obscured by the median fold, ending about 4/5 up; cells of apical blade narrowly rhomboidal or lenticular, up to 8μ wide by 25–45μ long, median cells similar but rather narrower, basal cells linear, up to 60μ long, rather incrassate throughout with firm, pellucid walls. Seta 10–12 mm. long, shorter in reduced forms, dark red, scabrous above and sometimes roughened to or below the middle; capsule erect, short oval, 1–1.25 mm. long by 0.7 mm. wide, dark brown, exothecal cells rounded, hexagonal, thick walled but not strongly collenchymatous except near the rim; peristome yellowish, densely papillose, teeth usually with several apertures along the median line; lid erect, rostrate, 0.75 mm. long, yellowish; calyptra slightly scabrous above, copiously fringed; spores roughened, 12–18μ in diameter.

Type Locality: Colombia, Boqueron.

Distribution: Colombia, Galapagos Islands, Ecuador.

Material seen: COLOMBIA: Boqueron, 2100 m., *Lindig 2023* (type); Boqueron prope Bogota, *Weir 193, 294, 336, 338;* Paramo El Boqueron bei Bogota, *K. Troll*

2180d, 2185.—GALAPAGOS ISLANDS: Chatham Island, *Alban Stewart 2782.*—ECUADOR: Andes Quitenses, Cayembe, *Spruce.*

Remarks: Evidently Mitten was unaware of Hampe's species, as there is no reference to it in his Musc. Austro-Am. published in 1869. Lindig's type collection and the subsequent collections of Weir and Troll all come from the Paramo Boqueron near Bogota, and are identical in every essential particular. *Weir 336* and *Troll 2180d* seem to be only stunted forms without any structural differences, and the plants collected by Stewart in the Galapagos Islands are likewise inseparable from those of the type locality. The species may be recognized by the elongated, firm basal cells blending with the border, which is consequently ill-defined below, and by the axillary propagulae. *D. stenophylla* is a smaller plant with narrower leaves. Some forms of *D. Lindigiana* are uncomfortably close to *D. gracilis*, in fact the four species *D. stenophylla*, *D. gracilis*, *D. Hampeana* and *D. ovalis* form a rather compact group of closely related forms that are often difficult to delimit sharply, but for the present it does not seem that any constructive result will be gained by further condensation.

10. DALTONIA STENOPHYLLA Mitt. Jour. Linn. Soc. Bot. **12**: 402. 1869.

D. aristifolia Bartr. Cont. U. S. Nat. Herb. **26**: 99. 1928; *D. Fendleri* C. Müller Linnaea **42**: 491. 1879; *D. tenella* Broth. Act. Soc. Sci. Fenn. no. 5. 1897.

Autoicous. Plants in small tufts, pale green, glossy. Stems short and slender, simple or branched, 5–12 mm. high, 1–2 mm. broad with leaves, radiculose below. Leaves closely imbricated, straight or lightly twisted when dry, carinate with a narrow median fold, narrowly linear-lanceolate, subulate acuminate, up to 3 mm. long by 0.3 mm. wide at base; margin narrowly revolute, entire; border pellucid, rather indistinct below, 5–8 rows wide at base, 4–6 rows wide at mid-leaf and 2 rows wide above; costa about 40μ wide at base channelled, ending about 4/5 up; cells of apical blade lenticular, about 7μ wide and up to 45μ long, median cells similar, basal cells linear-oblong, up to 70μ long, firm throughout with slightly thickened, pellucid walls. Seta up to 9 mm. long, often shorter, reddish, slightly scabrous above; capsule erect, narrowly oval, up to 1.2 mm. high by 0.5 mm. wide, dark brown, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose; lid erect, rostrate, 0.75 mm. long, yellowish; calyptra nearly smooth above, fringed; spores minutely roughened, 10–12μ in diameter.

Type Locality: Mt. Tunguragua, Ecuador.

Distribution: Jamaica; St. Vincent; Costa Rica; Venezuela; Ecuador; Brazil.

Material seen: JAMAICA: Dollwood, St. Catharine's Peak, *Nichols 94;* Blue Mt. Peak, *Jaderholm 7420.*—ST. VINCENT: *Guilding.*—COSTA RICA: Volcan de Turrialba, *Standley 35156a.*—VENEZUELA: Valencia, *Fendler 131.*—BRAZIL: Caraca, Minas Geraes, *Wainio;* Alto de Serra, San Paulo, *A. Gehrt 466, 469,* com. Herzog.—ECUADOR: Mt. Tunguragua, *Spruce 568* (type); Llalla, *Spruce 567.*

Remarks: The plants included here vary in the degree of robustness and length of setae but they all have in common the nearly erect, subulate-acuminate leaves, elongated pellucid leaf cells and rather narrow, poorly defined border below. Axillary, septate propagulae, similar to those found in *D. Lindigiana* but small, occur sparingly in no. 466 from Brazil, but otherwise the plants of this collection are indistinguishable from those included in the specific concept of *D. stenophylla*.

11. DALTONIA BILIMBATA Hampe Linnaea **32**: 151. 1863.

D. compressa Mitt. Jour. Linn. Soc. Bot. **12**: 400. 1869.

Autoicous. Plants densely tufted, yellowish green above, brown below, glossy. Stems up to 1.5 cm. high, rather robust, simple, about 5 mm. wide with leaves, radiculose below. Leaves crowded, erect-spreading, slightly flexuose, carinate with a median fold, oblong-lanceolate, acuminate, 4 mm. long by 0.5 mm. wide at base; margin narrowly revolute on one or both sides, entire; border pellucid, very broad and distinct in the lower half and occupying 1/2 or more of the leaf base, 12–15 rows wide at base, 7–9 rows wide at mid-leaf and 2–3 rows wide above; costa about 45μ wide at base, ending about 4/5 up; cells of apical blade oval-hexagonal to oval-rhomboidal, about 8μ wide by 25–30μ long, median cells similar, basal cells rather lax, rectangular and linear-oblong, all rather thin walled and hyaline. Seta slender, reddish, up to 14 mm. long, indistinctly roughened or smooth above; capsule inclined, narrowly oval, about 2 mm. long by 0.9 mm. wide, dark brown, exothecal cells collenchymatous in upper half of urn, uniformly thickened below; peristome normal; lid erect, rostrate, 1.5 mm. long, yellowish; calyptra slightly rough above, fringed; spores roughened, 20–25μ in diameter.

Type Locality: Bogota, Colombia.

Distribution: Colombia, Ecuador.

Material seen: COLOMBIA: Bogota, Monserate, *Lindig* (type); Grenze der 'Ceja' gegen den Paramo, *K. Troll 2028;* Andes Bogotenses, *Weir 349.*—ECUADOR: Mt. Pichincha, *Spruce 563.*

Remarks: The robust habit, long leaves and wide border clearly distinguish this species from any others in the group with revolute leaf margins. The margin in this species varies somewhat, being sometimes narrowly revolute on one side and broadly recurved on the other or even flat toward the base, but never plane throughout as in *D. longifolia* and its allies.

12. DALTONIA PELLUCIDA Herzog, Bibl. Bot. 87: 128. 1916.

Autoicous. Plants in small, dense tufts, yellowish green above, brown below, glossy. Stems up to 2.5 cm. high, about 2.5 mm. wide with leaves, simple or branched, densely radiculose below. Leaves crowded, erect and spirally twisted when dry, erect-flexuose when moist, carinate with a median fold,

oblong-ligulate, up to 4 mm. long by 0.75 mm. wide at base; margin narrowly revolute, more broadly so on one side than the other, entire; border pellucid, well defined, 7–9 rows wide at base, 5–7 rows wide at mid-leaf and 2 rows wide above; costa 40μ wide at base, ending about 4/5 up; cells of apical blade oval-hexagonal, scarcely incrassate, 7–8μ wide by 15–25μ long, median cells similar but more oblong, basal cells oblong and linear-oblong, all pellucid. Seta up to 1 cm. long, slender, reddish, smooth; capsule oval, 1.5 mm. high by 1 mm. wide, dark brown; peristome, lid and calyptra unknown; spores roughened, about 15μ in diameter.

Type Locality: Comarapa, Bolivia.
Distribution: Endemic.
Material seen: Bolivia: Auf Baumästen im Nebelwald über Comarapa, ca. 2600 m., *Herzog 4214* (type).

Remarks: This plant together with *D. peruviana* and *D. bilimbata* form a natural little group characterized by the robust habit and broadly bordered leaves. *D. pellucida* may be distinguished from *D. peruviana* by the smooth seta, and from *D. bilimbata* by the narrower border and shorter, broader capsules.

13. DALTONIA PERUVIANA Mitt. Jour. Linn. Soc. Bot. **12**: 401. 1869.

Autoicous. Plants densely tufted, pale yellowish green above, brown below, slightly glossy. Stems rather robust, up to 2.5 cm. high, about 2 mm. wide with leaves, cuspidate at the tips, radiculose below. Leaves crowded, erect, flexuose and twisted when dry, carinate with a median fold, oblong-lanceolate, acuminate, up to 3 mm. long by 0.8 mm. wide at base; margin narrowly revolute, entire; border pellucid, broad and well defined, 12–15 rows wide at base, 7–9 rows wide at mid-leaf and 2–3 rows wide above; costa 35μ wide at base, ending about 4/5 up; cells of apical blade oval-hexagonal, 7μ wide by 15–20μ long, not incrassate, pellucid, median cells similar but more hyaline, basal cells oblong, hyaline. Seta slender, 8 mm. long, reddish, rough above; capsule erect or inclined, oval, 1 mm. high by 0.5 mm. wide, brown; peristome, lid and calyptra unknown(capsules all old).

Type Locality: Cordillera de Raneo, Sachapata, Peru.
Distribution: Endemic.
Material seen: Peru: Cordillera de Raneo, Sachapata, *Lechler* (type).

Remarks: The wide border and hyaline areolation suggest an approach to *D. bilimbata*, but that species is even more robust with longer, more broadly bordered leaves and in addition has an almost smooth seta and much larger capsules.

14. DALTONIA LATOLIMBATA Broth. Bibl. Bot. 87: 129. 1916.

Autoicous? Plants in small tufts, golden green above, pale brown below, glossy. Stems rather robust, about 2 cm. high, simple or branched, 3–4 mm.

wide with leaves, radiculose below. Leaves crowded erect-spreading and lightly twisted when dry, more widely spreading and somewhat flexuose when moist, carinate with a small median fold, oblong-lanceolate, gradually acuminate, up to 4 mm. long by 0.9 mm. wide at base; margin narrowly revolute, often merely reflexed or even flat in acumen, entire; border pellucid, rather indistinct, 12–15 rows wide at base, 7–9 rows wide at mid-leaf and 2–3 rows wide above; costa 45μ wide at base, ending about 4/5 up; cells of apical blade with oval lumens, incrassate, pellucid, about 7μ wide by 20μ long, median cells similar but more elongated becoming linear toward costa, basal cells between border and central band linear-oblong and linear-rhomboidal, incrassate and pellucid, a band 8 or 10 rows wide on either side of costa very long and narrow, similar to the border cells. Seta about 7 mm. long, slender, reddish, slightly rough above; capsule erect, oval, about 1.1 mm. high; peristome, lid and calyptra unknown; spores (ex desc.) 25μ in diameter.

Type Locality: Incacorral, Bolivia.
Distribution: Endemic.
Material seen: Bolivia: Incacorral, 2200 m., *Herzog 4950a* (type).

Remarks: The rounded, incrassate cells of the upper lamina distinguish this species at once from any others in the group of robust plants with broadly bordered leaves and revolute margins. The band of long, narrow cells next to the costa extending from the base to above mid-leaf is a very marked character shared by only one other species, *D. brevinervis*, which is distinguished at a glance from *D. latolimbata* by the linear upper leaf cells, short nerve and narrow border.

15. DALTONIA TRACHYDONTIA Mitt. Jour. Linn. Soc. Bot. **12**: 400. 1869.

D. subirrorata Broth. Bibl. Bot. 87: 129. 1916. *D. Valdiviae* Herzog, Hedwigia **64**: 15. 1923.

Autoicous. Plants in small tufts, fulvous green, glossy. Stems up to 1 cm. high, about 1 mm. wide with leaves, radiculose below. Leaves crowded, erect flexuose and twisted when dry, erect-spreading and flexuose when moist, carinate with a broad median fold, oblong-ligulate, acuminate, up to 3 mm. long by 0.4 mm. wide at base; margin narrowly revolute, often more broadly so on one side, entire; border pellucid, narrow but well defined, 3–5 rows wide at base, 2–3 rows wide at mid-leaf and 1–2 rows wide above; costa slender, obscured by median fold, 30μ wide at base, ending about 3/4 up; cells of apical blade oval-hexagonal, not incrassate, rather pellucid, about 7μ wide by 14–18μ long, median cells similar, more rhomboidal, basal cells oblong, up to 25μ long. Seta up to 1 cm. long, reddish, smooth or nearly so; capsule erect, oval, up to 1.5 mm. long by 0.5 mm. wide, peristome yellowish, densely papillose; lid rostrate, erect, 0.75 mm. long, yellowish; calyptra smooth above; spores roughened, 12–16μ in diameter.

Type Locality: Cayembe, Andes Quitenses, Ecuador.

Distribution: Ecuador, Bolivia, Chile.

Material seen: ECUADOR: Cayembe, Andes Quitenses, cum *D. ovalis*, *Jameson* (type).—BOLIVIA: Sorata, 2500 m., *Williams 2942;* Aucoma, Cordillera Real, ca. 4000 m., *K. Troll 27*.—CHILE: Arique, Isla de Tejas, bei Valdivia, *Herzog 5268*.—BOLIVIA: Incacorral, *Herzog 5091a* in part.

Remarks: Distinguished from *D. tenuifolia* by the broader, more ligulate leaves, wider capsule and especially by the rather incrassate, pellucid leaf cells which are short and firm at the base. Having been unable to separate the Bolivian plants described by Brotherus from those representing the type collection of *D. trachydontia* I have no alternative but to include them under the older specific name. I have also been tempted to refer *D. Valdiviae* to synonymy, as it seems to be only a reduced form differing from the type in no important particular but the shorter seta. This is a variable factor at best, and hardly strong enough alone to merit a specific distinction.

16. DALTONIA TENUIFOLIA Mitt. Jour. Linn. Soc. Bot. **12**: 402. 1869.

Autoicous. Plants in small tufts, sordid to bright green, glossy. Stems slender, up to 7 mm. high, simple or branched, 1–1.5 mm. wide with leaves, radiculose below. Leaves crowded, erect, flexuose and lightly twisted when dry, erect-spreading and flexuose when moist, carinate, linear-lanceolate, slenderly acuminate, up to 2.5 mm. long by 0.3 mm. wide at base; margin narrowly revolute on one or both sides toward base, usually flat in acumen, entire; border pellucid, rather narrow, 4–6 rows wide at base, 3–4 rows wide at mid-leaf and 1–2 rows wide above; costa 40μ wide at base, obscured by the narrow median fold, ending about 4/5 up; cells of apical blade oval-hexagonal, lax, not incrassate, up to 12μ wide by 25μ long, median cells more rhomboidal, basal cells linear-oblong, thin walled, delicate and hyaline. Seta up to 6 mm. long, reddish, smooth; capsule erect, oval-cylindrical, 1–1.5 mm. high by 0.5 mm. wide, peristome yellowish, densely papillose; lid rostrate, erect, 0.6 mm. long, yellowish; calyptra smooth above, copiously fringed; spores roughened, 10–12μ in diameter.

Type Locality: Pallatanga, Andes Quitenses, Ecuador.

Distribution: Costa Rica, Ecuador, Bolivia.

Material seen: COSTA RICA: San Jose, Prov. San Jose, *M. Valerio 205a*.—ECUADOR: Pallatanga, ad arbores, 6000 ft., *Spruce 561* (type).—BOLIVIA: Quebrada de Pacona, 2800 m., *Herzog 5149*.

Remarks: For distinctions between this species and *D. trachydontia* refer to notes under the latter plant.

17. DALTONIA GRACILIS Mitt. Jour. Linn. Soc. Bot. **12**: 402. 1869.

D. Wallisii C. Müll. Flora **58**: 550. 1875; *D. ocanniana* C. Müll. Flora **58**:

551. 1875; *D. lorifolia* C. Müll. Flora **58:** 550. 1875; *D. minutifolia* C. Müll. Nuov. Giorn. Bot. Ital. **4:** 148. 1897; *D. Hampeana* Geheeb, Vidensk. Meddel. Kjøb. **1879–1880:** 122. 1879; *D. curvicuspes* C. Müll. Hedwigia **39:** 268. 1900; *D. Krauseana* C. Müll.

Autoicous and synoicous. Plants in small tufts, yellowish or fulvous green, glossy. Stems slender, up to 1 cm. high, about 1 mm. wide with leaves, radiculose below. Leaves crowded, erect, flexuose-twisted when dry, flexuose when moist, carinate with a narrow median fold, linear-lanceolate, up to 2.5 or 3 mm. long by 0.4 mm. wide at base; margin narrowly revolute on one or both sides, sometimes flat toward base, entire; border pellucid, well defined, 6–8 rows wide at base, 3–4 rows wide at mid-leaf and 2 rows wide above; costa 30μ wide at base, ending about 4/5 up; cells of apical blade lenticular or narrowly rhomboidal up to 7μ wide by 24μ long, slightly incrassate, pellucid, median cells similar, rhomboidal and linear rhomboidal, basal cells linear-oblong, hyaline. Seta slender, about 6 mm. long, reddish, scabrous above and sometimes rough half way down; capsule erect or inclined, oval-cylindrical, up to 1.1 mm. high by 0.5 mm. wide, dark brown, exothecal cells strongly collenchymatous; peristome yellowish, densely papillose; lid erect, rostrate, 0.75 mm. long, yellowish; calyptra slightly rough above, fringed; spores roughened, 12–14μ in diameter.

Type Locality: Canelos, Andes Quitenses, Ecuador.

Distribution: Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Chile, Brazil.

Material seen: COSTA RICA: Candelaria in foliis arboreum inter Hepaticas, *Oersted.*—PANAMA: Humid forest between Alto de las Palmas and top of Cerro de la Horqueta, Chirique, *Pittier 3252* in part.—COLOMBIA: Sibati to El Penon, *Rusby & Pennell;* Ocanna and Santa Isabel, *Wallis.*—ECUADOR: in sylva Canelos, Andes Quitenses, 3000 ft., *Spruce 560* (type).—PERU: Tatanara, *Lechler.*—BOLIVIA: Bergwald von Tocorani, *Herzog 4042;* Incacorral, *Herzog 5021;* Prov. Cochabamba prope Choquecamata, *Germain;* Rio Tocorani, *Herzog 4081d* in part; Incacorral *Herzog 18;* Estradillas, Prov. Cochabamba, *Herzog.*—CHILE: Valdivia, *Krause.*—BRAZIL: prope Apiahy, San Paulo, *Puiggari;* Serra Ouro Preto, Minas Geraes, *Ule 1438.*

Remarks: The plants referred here vary considerably in size but there are no structural differences that can be correlated with the smaller forms described by Müller under the names of *D. lorifolia* and *D. minutifolia* and it seems highly probable that all these collections are merely variants of one specific type. The margins are sometimes flat but not consistently so, as leaves with plane margins and others with one or both margins narrowly revolute are found on the same plant. There is nothing to distinguish either *D. Wallisii* or *D. ocanniana* from each other or from the type, and although *D. minutifolia* is a smaller plant more nearly resembling *D. splachnoides* of Europe, I have been unable to satisfactorily separate it from *D. gracilis.* This species has a broad distribution, and no doubt includes

D. Hampeana and *D. curvicuspes* of Brazil, in which the upper leaf cells are more elongated and the seta not quite so rough, but not uniformly enough to establish any satisfactory separation.

18. DALTONIA OVALIS Tayl. Lond. Jour. Bot. **5**: 66. 1846.

Autoicous. Plants up to 12 mm. high, about 1.5 mm. wide with leaves, radiculose below. Leaves crowded, erect-flexuose and slightly twisted when dry, flexuose when moist, carinate with a median fold, lanceolate, up to 1.75 mm. long by 0.27 mm. wide at base; margin narrowly revolute on one or both sides, sometimes flat toward base, entire; border pellucid, rather narrow, 4–5 rows wide at base, 3–4 rows wide at mid-leaf and 2 rows wide above; costa 30μ wide at base, ending about 3/4 up; cells of apical blade oval and oval-rhomboidal, 7μ wide by about 20μ long, slightly incrassate, pellucid, median cells similar, basal cells oblong and rhomboidal, about 1: 3. Seta slender, up to 14 mm. long, reddish, roughened above; capsule inclined, oval, dark brown, 1.1 mm. high by 0.5 mm. wide, exothecal cells collenchymatous near the rim and uniformly thickened below; peristome yellowish, densely papillose; lid rostrate, erect, 0.8 mm. long, yellowish; calyptra slightly rough above; spores roughened, 17–20μ in diameter.

Type Locality: Cayembe, Andes Quitenses, Ecuador.

Distribution: Endemic.

Material seen: Ecuador: Cayembe, Andes Quitenses, on shrubs, 1400 meters, *Jameson* (type).

Remarks: This species is known only from the type collection and may be distinguished from *D. gracilis*, which it approaches very closely, by the broader leaves, shorter basal cells and longer seta.

DOUBTFUL AND EXCLUDED SPECIES

DALTONIA CUCULLATA Hampe Linnaea **32**: 151. 1863. It is impossible to locate this species definitely from the description and no specimens have been available for comparison.

DALTONIA SERICEA Schimper, Ms. The specimen under this name in the herbarium of the New York Botanical Garden is mostly *Leucomnium attenuatum* Mitt., with some strands of *Taxithelium planum*. No *Daltonia* plants were found.

DALTONIA LONGICUSPIDATA C. Müll. Bull. Herb. Boiss. **5**: 201. 1897. What is supposed to be a part of the type collection, ex Hb. Brotherus, in the herbarium of the New York Botanical Garden does not agree with the description or the type locality cited by Müller. As no further material is available for comparison it seems best to exclude this species until its status can be definitely determined.

ALPHABETICAL LIST OF SPECIES

Daltonia androgyna Geh. & Hampe
Daltonia ariquensis Schimper = *D. gracilis* Mitt.
Daltonia aristata Geh. & Hampe
Daltonia aristifolia Bartr. = *D. stenophylla* Mitt.
Daltonia bilimbata Hampe
Daltonia binervis Hampe = *Lepidopilum daltoniacum* Ann. Sci. Nat. Bot. V. 4: 364. 1866.
Daltonia braziliensis Mitt.
Daltonia brevinervis Bartr.
Daltonia brevicuspidata Broth. = *D. longifolia* Tayl.
Daltonia compressa Mitt. = *D. bilimbata* Hampe
Daltonia crispata Schimper = *D. longifolia* Tayl.
Daltonia cucullata Hampe, excluded
Daltonia curvicuspes C. Müll. = *D. gracilis* Mitt.
Daltonia Dussii Broth. = *D. longifolia* Tayl.
Daltonia Fendleri C. Müll. = *D. stenophylla* Mitt.
Daltonia gracilis Mitt.
Daltonia Hampeana Geh. = *D. gracilis* Mitt.
Daltonia irrorata Mitt. = *D. Lindigiana* Hampe
Daltonia Jamesoni Tayl.
Daltonia Krauseana C. Müll. = *D. gracilis* Mitt.
Daltonia latolimbata Broth.
Daltonia leucoloma Hampe = *D. braziliensis* Mitt.
Daltinia Lindigiana Hampe
Daltonia longifolia Tayl.
Daltonia longicuspidata C. Müll. excluded
Daltonia lorifolia C. Müll. = *D. gracilis* Mitt.
Daltonia macrotheca Mitt.
Daltonia minutifolia C. Müll. = *D. gracilis* Mitt.
Daltonia ocanniana C. Müll. = *D. gracilis* Mitt.
Daltonia ovalis Tayl.
Daltonia pellucida Herz.
Daltonia peruviana Mitt.
Daltonia pulvinata Mitt.
Daltonia robusta Ångstr. = *D. longifolia* Tayl.
Daltonia sericea Schimper, excluded.
Daltonia stenophylla Mitt.
Daltonia Stewartii R. S. Williams = *D. Lindigiana* Hampe
Daltonia subirrorata Broth. = *D. trachydontia* Mitt.
Daltonia tenella Broth. = *D. stenophylla* Mitt.
Daltonia tenuifolia Mitt.
Daltonia trachydontia Mitt.
Daltonia Uleana C. Müll. = *D. aristata* Geh. & Hampe
Daltonia Valdiviae Herz. = *D. trachydontia* Mitt.
Daltonia Wallisii C. Müll. = *D. gracilis* Mitt.

BUSHKILL, PIKE COUNTY
PENNSYLVANIA

Explanation of plates 3, 4

The figures in the following plates are all drawn from plants representing the type collections. The following symbols are used uniformly throughout the plates:

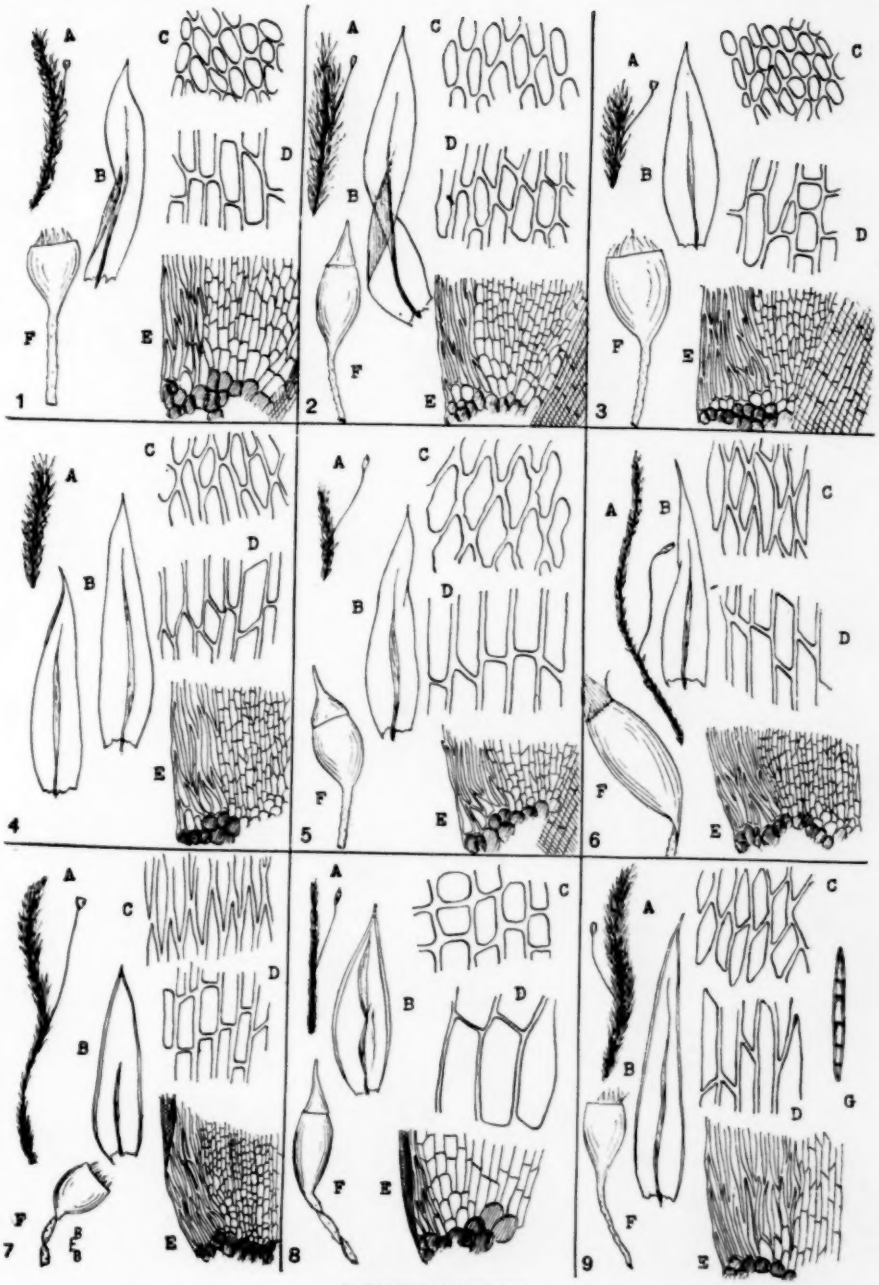
A—Plant ×2.
B—Leaf ×18.
C—Upper leaf cells ×400.
D—Basal leaf cells ×400.
E—One side of leaf base ×160.
F—Capsule ×12.
G—Propagula ×160.

Plate 3

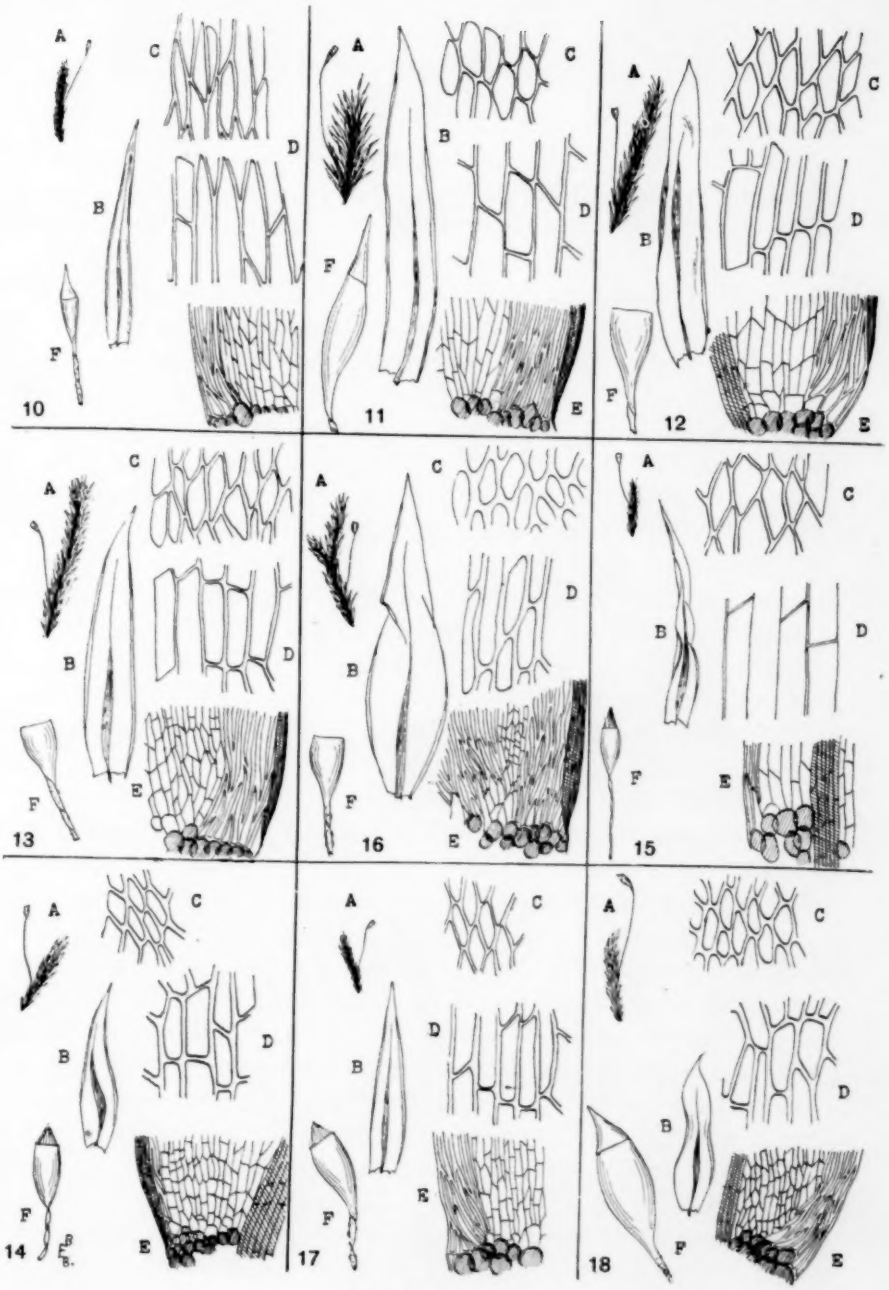
Fig. 1. Daltonia pulvinata Mitt.
Fig. 2. Daltonia longifolia Tayl.
Fig. 3. Daltonia braziliensis Mitt.
Fig. 4. Daltonia aristata Geheeb & Hampe
Fig. 5. Daltonia androgyna Geheeb & Hampe
Fig. 6. Daltonia macrotheca Mitt.
Fig. 7. Daltonia brevinervis Bartram
Fig. 8. Daltonia Jamesoni Tayl.
Fig. 9. Daltonia Lindigiana Hampe

Plate 4

Fig. 10. Daltonia stenophylla Mitt.
Fig. 11. Daltonia bilimbata Hampe
Fig. 12. Daltonia pellucida Herz.
Fig. 13. Daltonia peruviana Mitt.
Fig. 14. Daltonia latolimbata Broth.
Fig. 15. Daltonia trachydontia Mitt.
Fig. 16. Daltonia tenuifolia Mitt.
Fig. 17. Daltonia gracilis Mitt.
Fig. 18. Daltonia ovalis Tayl.



BARTRAM: DALTONIA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Nomenclatural notes[1]

H. C. Skeels

In a recent issue of *Gentes Herbarum* (vol. 2, fasc. 4, p. 170, 1930) Dr. L. H. Bailey lists the binomial *Eugenia paniculata* Banks as published by Gaertner, 'Fruct. et Sem. Plant. i, 167 t. xxxiii, no. 1 (1788),' and cites as a synonym *Syzygium paniculatum* Gaertn. l. c. This is an exact reversal of the facts. Gaertner published the binomial *Syzygium paniculatum* and cited as a synonym '*Eugenia paniculata* Hort. Sicc. Banks.' This is only a name on an herbarium sheet and has no more standing in botanical nomenclature than the two names *Eugenia Hookeri* and *E. Hookeriana* listed by Dr. Bailey as 'Hort.' *Eugenia paniculata* Lam., published in 1789 for a different species, as correctly reported by Dr. Bailey, is a tenable name for the species Lamarck described and precludes the use of that binomial for any other species in *Eugenia*. Similarly, *Eugenia myrtifolia* Salisb., 1796, precludes the use of *E. myrtifolia* Sims, 1821, for the species under discussion. The first tenable name so far known for this species is *Eugenia australis* Wendl., and this is the name at present used by the Department of Agriculture. If Dr. Bailey considers the form horticulturally known as *Eugenia Hookeri* distinct enough to deserve a subspecific name, it will be necessary to publish one, as this form is apparently without a name at the present time.

In the same publication, on page 192, Dr. Bailey has taken up the generic name *Stevensonia* Duncan, giving as the place of publication 'Van Houtte in Fl. des Serr. xv, 177, t. 1595–6 (1865).' I cannot agree with Dr. Bailey that this is publication for the generic name *Stevensonia*. While *Stevensonia Sechellarum* appears in boldface capitals under the figure on the plate, it is followed by 'Hort' in brackets, and *Phoenicophorium Sechellarum* appears at the side in larger type, although italic. In the text, which is the place that really constitutes publication, *Stevensonia grandifolia* Dunc. appears at the top of the page in parentheses, and the real heading, *Phoenicophorium Sechellarum* Herm. Wendl., appears just below it in boldface type twice the size of the type used for *Stevensonia*. And the generic and specific characterizations in Latin are both quoted from H. Wendland (Illust. Hort. **12**: Misc. 5).

On page 194, Dr. Bailey, mentioning the plate 433 appearing in Ill. Hort. in April, 1865, under the name *Phoenicophorium Sechellarum*, and the other plate of the same palm appearing in Flore des Serres in the same month, considers that the former probably antedates the latter since it is

[1] Published by permission of the Secretary of Agriculture.

quoted there, but states that 'it is unsafe to make such a decision, for Van Houtte may have seen an advance proof.' He apparently overlooked the fact that page 5 of the miscellany where the Latin characterization of the genus *Phoenicophorium* and the publication and Latin description of *P. Sechellarum* first appear, is dated février 1865, thus disposing of any doubt as to the date of the first properly published name for this species. If these characterizations written by Hermann Wendland and published in Ill. Hort. in February, 1865, and republished in Flore des Serres in April, 1865, for the generic name *Phoenicophorium*, are to be used in 1930 to validate the horticultural name *Stevensonia*, it will be the second steal in which this poor palm has innocently figured. I am especially interested in the correct name for this palm, as the last citation given by Dr. Bailey, *Phoenicophorium borsigianum* Stuntz, was based on work done by Mr. Stuntz and myself in 1914 on this species, and the name then adopted is now being used by the Department of Agriculture.

Unless Dr. Bailey has reasons more adequate than are evident from examining documents now available to the writer, it would appear that in spite of his great prestige, the recognition which he has given to these names listed in synonymy, *Eugenia paniculata* Banks and *Stevensonia* Dunc., should not be accepted by botanists generally.

UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

INDEX TO AMERICAN BOTANICAL LITERATURE

1927–1931

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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